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LARVAL HOSTS OF *ANAPLECTOIDES* AND *APLECTOIDES* WITH NOTES ON THEIR BIOLOGY (LEPIDOPTERA: NOCTUIDAE)

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Abstract.—The larva of *Aplectoides condita* Guenée (Lepidoptera: Noctuidae) is described and illustrated. *Larix laricina* (Du Roi) Koch was found to be an acceptable host. The species is univoltine and normally overwinters as a larva in a cocoon. An unusual adult form of *condita* is illustrated. The larva of *condita* is compared to that of *Anaplectoides pressus* (Grote). *Larix laricina*, *Sambucus canadensis* L., *Salix gracilis* Anderss., *Vicia cracca* L., *Betula papyrifera* Marsh and *Alnus rugosa* Du Roi, represent new host records for *pressus*.

Tietz (1972) gave host records for *Aplectoides condita* Guenée, but in actuality the hosts listed were for *Jocara trabalis* Grote, a pyralid. Smith (1893) first recognized the synonymy between *Agrotis trabalis* Grote, a noctuid, and *Aplectoides condita*, but Tietz inadvertently treated the other Grote *trabalis* species, *Jocara trabalis*, as the synonym, hence the incorrect host citation.

Grote (1877) described *trabalis* from two specimens from Montreal and Massachusetts. Thaxter, who provided Grote with the type specimen of *trabalis*, gave the following (Grote, 1877) field notes: "cocoon found under pine bark in April, when the larva had not yet become pupa. The cocoon was tough, not unlike that of *cerura*. Larva dull white with blackish markings." The "dull white" descriptor probably was based on a prepupa as it bears no resemblance to the normal last instar larva. Confined larvae also made a cocoon on the bark. The larva may habitually form a cocoon on the trunk of the host which would add the "pine" of Thaxter to the list of acceptable hosts. Balsam, *Abies balsamea* (L.) Mill., was reported as a host for *condita* in Prentice (1962).

A female of *condita* was collected in the Adirondack Mountains on 3 June 1977. The moth oviposited two days later and in another eight days the larvae began to eclose. The first instar larvae were offered *Larix laricina* (Du Roi) Koch [Pinaceae] which they readily accepted. *Abies balsamea* [Pinaceae] was fed on to a much lesser extent, and *Pinus strobus* L. [Pinaceae], *Betula papyrifera* Marsh and *Alnus rugusa* Du Roi [Corylaceae], *Sambucus canadensis* L. [Caprifoliaceae], *Prunus virginiana* L. and *Spiraea latifolia* (Ait.) Borkh. [Rosaceae], and *Salix bebbiana* Sarg. [Salicaceae] were all avoided. Larvae were reared in continuous darkness interrupted by the addition of fresh *Larix* needles every two days. Full-grown larvae were obtained by 15 August. The larva normally overwinters in a cocoon amongst the needles or on the bark; the cocoon consists of bits of chewed bark and silk. Four males and two females pupated in the late summer and emerged in October and November, but the majority diapaused as larvae. Since the moth normally appears in June, the artificial rearing conditions had accelerated development and disrupted the normal larval diapause.
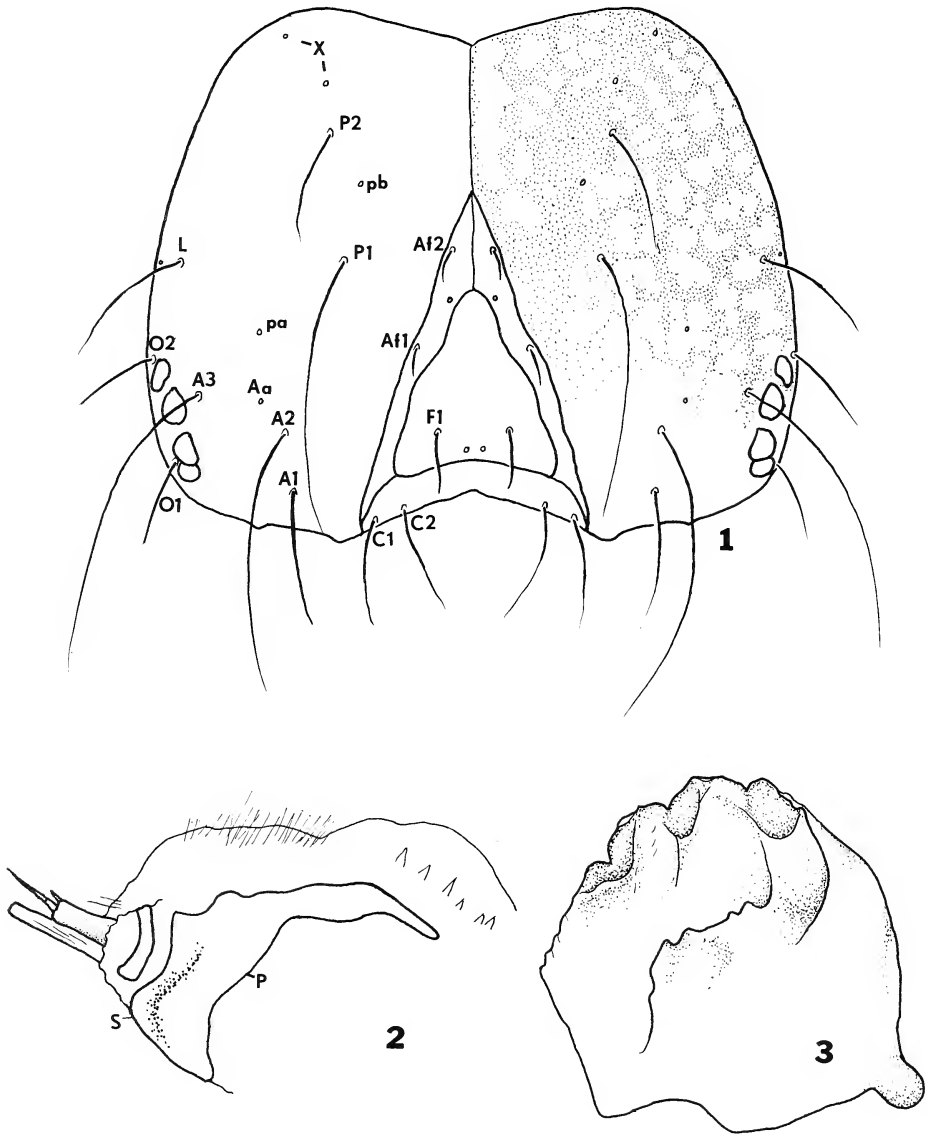
Figs. 1–3. *Aplectoides condita.* 1. Setal map of head capsule. 2. Hypopharynx. 3. Oral face of left mandible.

The larva of *condita* (Fig.4) can be distinguished from the related and frequently sympatric *Anaplectoides pressus* (Grote) by the squarish, black subdorsal patches (Fig. 5) and the deeply cleft mandibular teeth of *pressus*. Both species' larvae have similar proximolateral teeth on the hypopharynx, but *pressus* has the prementum deeply notched anterodorsally whereas *condita* is simple. Both larvae gradually in-

crease in width posteriorly. Crumb (1956) described the larva of *pressus* and gave Cornsalad (*Valerianella* sp.) as a host. Larvae of *pressus,* which I reared ex ova obtained from an Adirondack specimen, accepted *Larix laricina, Sambucus canadensis* L. (reared to maturity on this), *Salix gracilis* Anderss., *Vicia cracca* L. [Leguminosae], *Betula papyrifera* Marsh, and *Alnus rugosa* Du Roi, but would not feed on *Abies balsamea, Pinus strobus,* or *Tsuga canadensis* (L.) Carr. *Anaplectoides prasina* (Denis and Schiffermüller) is also polyphagous. If Crumb's (1956) keys are used, *condita* will not key to *pressus* because of the dissimilar proportion of the 2nd and 3rd labial segments. In *pressus* these two segments are both short and subequal whereas in *condita* segment 3 is four times the length of segment 2. The larvae of *pressus* and *condita* are nearly identical in head, thorax, and abdominal chaetotaxy. According to McDunnough (1923), in his generic revision of the North American agrotids, *Aplectoides* and *Anaplectoides* are placed together, sharing a modified *Agrotis* type of harpe and having the fore tibial spining much reduced. He states they are similar in outward structural characters but differ markedly in genitalic characters.

The adult of *condita* is illustrated in Figure 8. A most unusual form of *condita* was collected on 6 June 1980 on a bog on the south end of Raquette Lake, Hamilton County, New York. This form (Fig. 9) differs from a normal adult (Fig. 8) in being highly contrasty and lacking the brown scaling between the postmedian and subterminal lines. The genitalia was examined to confirm its identity. This single example was collected in the field a full week before normal *condita* began emerging.

Description of the mature larva of *Aplectoides condita*
(Setal nomenclature follows Hinton, 1946)

General (Fig. 4): Average head width 2.58 mm; average total length 33.0 mm; abdominal prolegs represented on 3rd through 6th and 10th segments; setae simple; spiracle Ab8 0.32 mm high on average (N = 6). Body gradually enlarged posteriorly.

Coloration (living material)(Fig. 4): Light brown, mottled and reticulate with dark brown, the most distinctive of these markings being a series of lateral abdominal patches passing through each spiracle and sloping downward toward the rear of each segment. Dorsal surface of each segment bearing a diamond-shaped patch which runs from segmental membrane to segmental membrane.

Head (Fig. 1): Epicranial suture 0.87 mm long; height of frons 0.94 mm. First adfrontal (Af1) posterior to apex of frons. Coronal punctures Fa, Afa, Aa, pa, pb, La, and 4 ultraposteriors (visible in frontal view, labeled with an "x") present as illustrated.

Mouthparts. Hypopharyngeal complex (Fig. 2): Labial palpi with 3rd segment four times length of 2nd; 2nd and 3rd and combined subequal to basal segment. Spinneret shorter than labial palpi; distal apex of hypopharynx bears a few setae, followed by a patch of setae and finally a posterior row of 6 or 7 widely spaced spines. Mandible (Fig. 3) with basal tooth present, outer teeth low.

Thoracic segments. Prothorax (Fig. 6): Cervical shield weakly scelerotized. All setae lacking pinaculi. SV group with two, or rarely one, setae. Meso- and metathorax with D2 and SD1 setae each accompanied by a puncture immediately below setal base. Only one subventral seta present.

Abdominal segments. Ab1 (Fig. 7): Two subventral setae (SV1 & SV3); L1 posterior
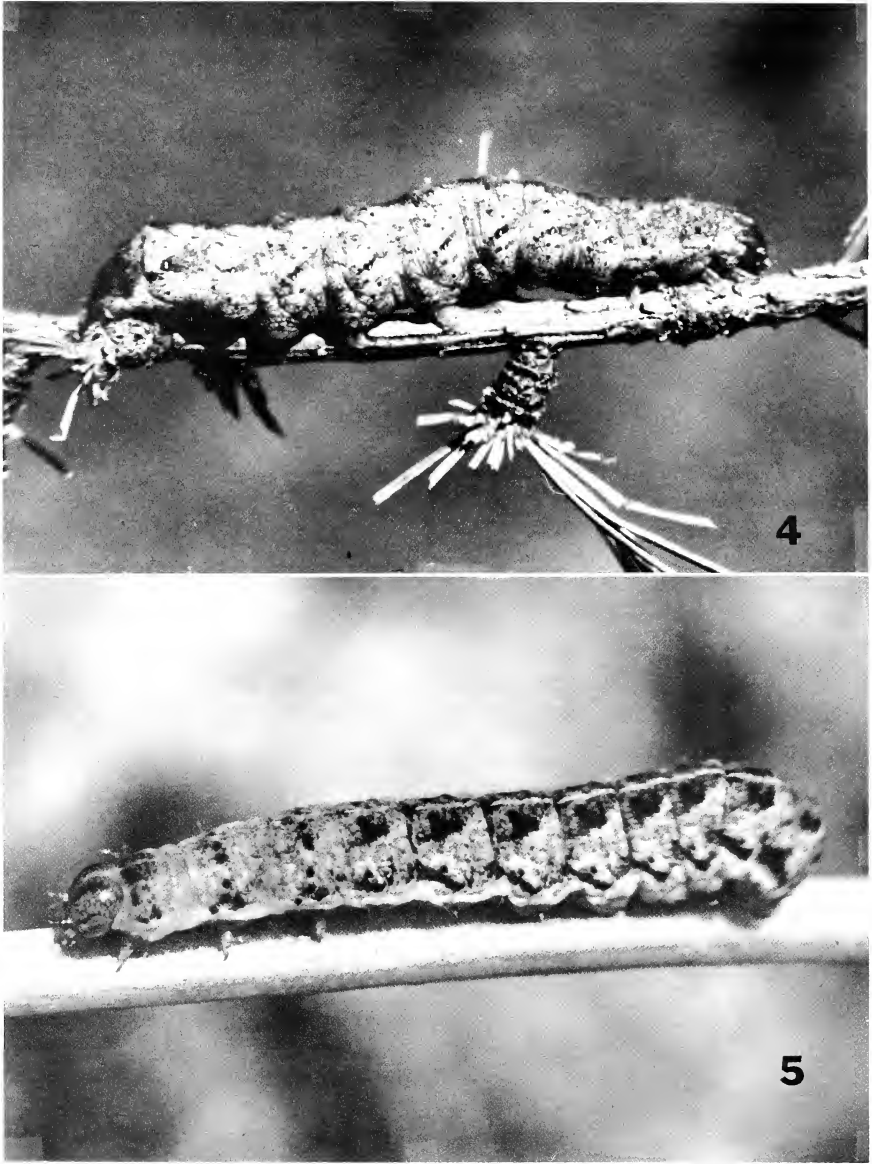
Figs. 4–5.   4. Mature larva of *Aplectoides condita.* 5. Mature larva of *Anaplectoides pressus.*

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Figs. 6–9.   *Aplectoides condita.* 6. Setal map of prothoracic segment (lateral view from mid-dorsal to midventral line). 7. Setal map of first abdominal segment (lateral view from middorsal to midventral line). 8. Bred adult *condita* from Indian Lake site. 9. Unusual adult form of *condita* taken on a bog on Raquette Lake, Hamilton County, New York.
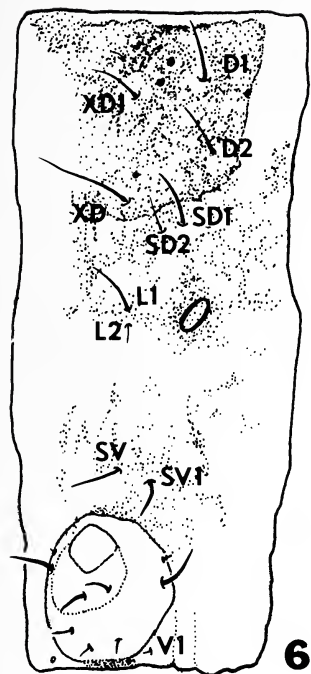
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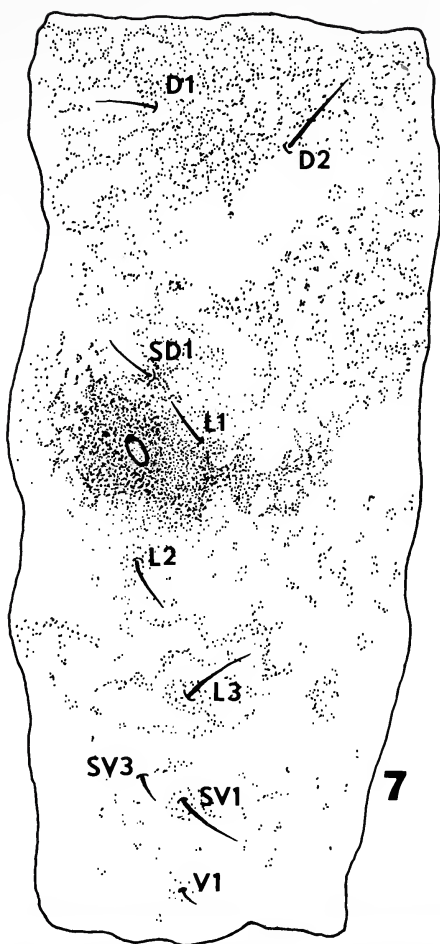
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9

to spiracle; SD2 seta absent, its setal base present anterior to spiracle. Ab2–Ab6 with 1 subventral seta; SD1 anterodorsal to spiracle; L1 posterior to spiracle. Ab7 with SD1 posterodorsal to spiracle; L1 posteroventral to spiracle; SV1 ventral to L2. Ab8 with SD1 posterodorsal to spiracle; L1 posterior to spiracle; SV1 posterodorsal to L2. Crochets a uniordinal mesoseries; 19–25 on Ab3, 18–28 on Ab4, 24–31 on Ab5, 25–30 on Ab6, and 32–35 on Ab10.

Material examined: 6 specimens, 10 kilometers east of Indian Lake, lat. 43°45′30″ long. 74°10′14″, Hamilton County, New York, elev. 555 meters, from ova of female collected and determined by T. L. McCabe. Parental female, all larvae, and F1 adults are coded tlm 77-47a. In 1980, another brood (tlm 80-96) from the same site was also used for host preference studies.

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RHYSODINI OF SULAWESI AND NEARBY ISLANDS (COLEOPTERA: CARABIDAE OR RHYSODIDAE)

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Abstract.—A key to the Rhysodini of Sulawesi and the nearby Banggai Archipelago is provided. Six new species are described and illustrated: *Omoglymmius* (*s. str.*) *ferrugatus,* from Banggai, and the remainder from Celebes: *Plesioglymmius* (s. str.) *moorei, Omoglymmius* (s. str.) *wallacei, O.* (s. str.) *brendelli, O.* (s. str.) *seriatus* and *O.* (*Indoglymmius*) *astraea.* Comparisons are made with the two species previously recorded from Sulawesi, and a key to all eight species is included.

Up to the present, only two specimens of Rhysodini have been known from the large and zoogeographically important island of Sulawesi (formerly Celebes), the holotypes of *Rhyzodiastes* (*Temoana*) *singularis* (Heller) and *Omoglymmius* (s. str.) *repetitus* Bell and Bell. Recently we have studied Rhysodini collected during Project Wallace, an intensive exploration of the fauna of Sulawesi, involving personnel of the British Museum of Natural History, the National Museum of New Zealand, and the Commonwealth Scientific and Industrial Research Organization of Australia. This material has revealed six additional species, giving a clearer though still fragmentary picture of the rhysodine fauna of the island.

At present, we have published four parts of a five part monograph of the Rhysodini of the world (Bell and Bell, 1978, 1979, 1982, 1985). Part I (1978) includes a discussion of the phylogeny of the group and a glossary of morphological terms. Part V, not yet completed, will include a discussion of the zoogeography of the group, as well as some minor revisions of the phylogeny.

A preliminary discussion of the zoogeography of the group has already been published (R. T. Bell, 1979). Subgenera represented in Sulawesi include *Omoglymmius* s. str., *Omoglymmius* (*Indoglymmius*), *Plesioglymmius* s. str., and *Rhyzodiastes* (*Temoana*). *Omoglymmius* s. str. includes more than 70 species, distributed from the Solomon Islands to Europe. Three of the four species have their closest relationships with species of the Moluccas and New Guinea, suggesting relatively recent spread from the east. The fourth, *O. brendelli,* is clearly related to species of the Greater Sunda Islands and the Philippines, suggesting invasion from the north or west. *Omoglymmius* (*Indoglymmius*) has only two species, one in southern India, the other in Sulawesi, an enigmatic distribution. *Plesioglymmius* s. str. has three species, one in Borneo and Sumatra, one in Mindanao, and the third in Sulawesi. The species from Mindanao is clearly closest to that from Sulawesi, suggesting recent spread from the north. *Rhyzodiastes* (*Temoana*) has 25 species, distributed from northern Australia, the Solomon and Caroline Islands to eastern India. The species from Sulawesi is closest in morphology to a species from New Guinea. It may have reached Sulawesi from the east. This conclusion is very tentative, since there are probably many species of this subgenus still awaiting discovery.

KEY TO RHYSODINI OF SULAWESI AND BANGGAI

1. Minor setae of antennae confined to tufts on ventral surface of segments 5–10; each elytron with only four striae, innermost stria distinct only in basal half of elytron (CLINIDIINA) .... *Rhyzodiastes* (*Temoana*) *singularis* (Heller)
–   Minor setae forming complete ring near apex of segments 5–10; each elytron with seven striae. (OMOGLYMMIINA) 2
2. Paramedian grooves of pronotum incomplete anteriorly, not attaining anterior margin .... *Plesioglymmius* (s. str.) *moorei* n. sp.
–   Paramedian grooves complete (*Omoglymmius*) 3
3. Eyes large, round; temporal lobe without translucent area along medial margin. (*Omoglymmius* s. str.) 4
–   Eyes virtually absent, represented only by indistinct paler areas; temporal lobe with translucent area along medial margin ..... *Omoglymmius* (*Indoglymmius*) *astraea* n. sp.
4. Temporal seta absent; lateral margin of inner carina of pronotum gradually sloped to paramedian groove .... *Omoglymmius* (s. str.) *seriatus* n. sp.
–   Temporal seta present; lateral margin of inner carina sharply defined 5
5. Postorbital tubercle present; pronotal carinae nearly impunctate, with very few, very fine punctures .... *Omoglymmius* (s. str.) *repetitus* Bell and Bell
–   Postorbital tubercle absent; outer carina coarsely, densely punctate, inner one varied   6
6. Median lobe, antennal lobes densely microsculptured, dull; base of elytral Stria 4 formed into scarp; inner carina with 10–15 fine punctures .... *Omoglymmius* (s. str.) *ferrugatus* n. sp.
–   Median lobe, antennal lobes shining, not microsculptured; base of Stria 4 not formed into scarp; inner carina with 5 or fewer punctures 7
7. Frontal grooves dilated, median lobe narrow, broadly separated from temporal lobes; inner pronotal carina with 1–5 coarse punctures near middle .... *Omoglymmius* (s. str.) *wallacei* n. sp.
–   Frontal grooves narrow, median lobe broad, narrowly separated from temporal lobes; inner carina with 1 minute puncture .... *Omoglymmius* (s. str.) *brendelli* n. sp.

Rhyzodiastes (*Temoana*) *singularis* Heller, 1898

Clinidium singulare Heller, 1898:3.
Rhyzodiastes singularis: Bell and Bell, 1978:61.
Rhyzodiastes (*Temoana*) *singularis*: Bell and Bell, 1985:27.

Bell and Bell (1985) provide a detailed description and figure of this species, still known only by the holotype, a female. The most closely related species is *Rhyzodiastes* (*Temoana*) *guineensis* (Grouvelle) of New Guinea. The type locality "Lompa-Battau" is probably a variant spelling of Lampobatang, a mountain at 5°20′S, 119°55′E, near Bonthain in the Southern Peninsula of Sulawesi. The area is an isolated mountain range, connected to the remainder of Sulawesi only by very lowlands, and has probably been a separate island at times. Other species of this subgenus are likely to be found in Sulawesi.

Plesioglymmius (s. str.) moorei, new species

Type material. Holotype male (Figs. 1, 2), "Indonesia, Sulawesi Utara, Dumoga-Bone N.P. Project Wallace 1985, lowland forest, Toraut vi. B. P. Moore" (CSIRO). Paratypes 6 females, from same locality, but dated September 1985 (NMNZ). This series was collected by Dr. R. Hornabrook, a fact not indicated on the label.
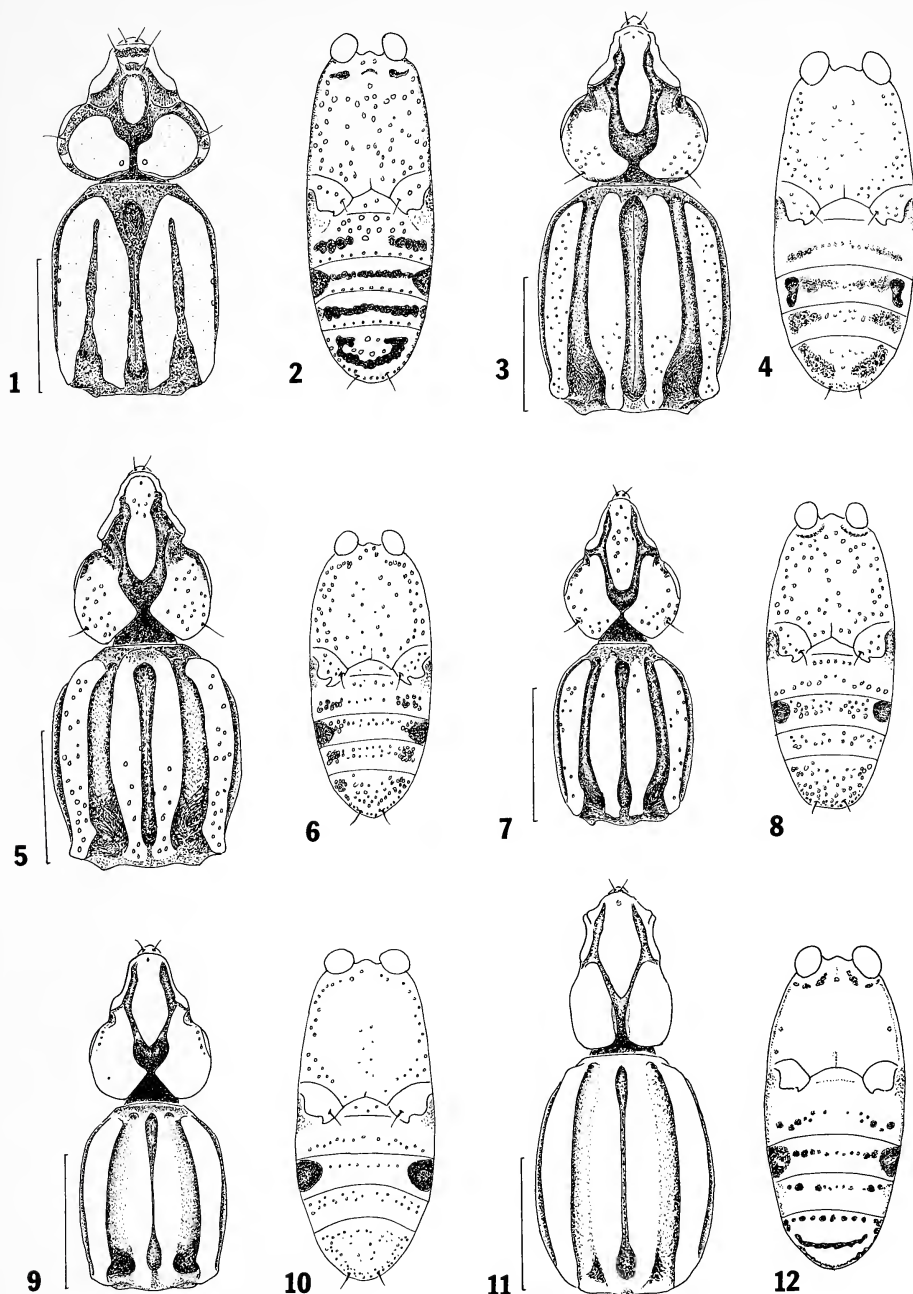
Figs. 1–12. Dorsal view of head and pronotum, ventral view of female metasternum and abdomen. 1, 2. *Plesioglymmius* (s. str.) *moorei*. 3, 4. *Omoglymmius* (s. str.) *ferrugatus*. 5, 6. *Omoglymmius* (s. str.) *wallacei*. 7, 8. *Omoglymmius* (s. str.) *brendelli*. 9, 10. *Omoglymmius* (s. str.) *seriatus*. 11, 12. *Omoglymmius* (*Indoglymmius*) *astraea*.

Description. Length 5.1–7.3 mm; head clearly broader than long; antennal stylet short, conical; clypeus as described for *P. silus* Bell and Bell of Mindanao; temporal lobe with 1–2 punctures near medial margin; 1 temporal seta, near posterior end of temporal groove, latter broadly pollinose; postorbit thickly pilose, without visible punctures; 1 postorbital seta opposite middle of eye (unilaterally absent in 2 specimens); mentum of male entirely pollinose except for anterior margin; mentum of female with central area glabrous, remainder pilose; 1 pair of postlabial setae.

Pronotum relatively short, length/width about 1.36; lateral margins parallel, not narrower posteriorly, as in *P. silus* Bell and Bell of Mindanao; pronotal grooves as in *P. silus*; outer carina with few coarse punctures near lateral margins, and many very fine, scattered punctures; notopleuron glabrous, margined with pilosity; prosternum pilose; prosternal process coarsely punctate, not pilose except for line of punctures and pollinosity on midline.

Elytral striae coarsely punctured, punctures not connected by pollinosity; metasternum in both sexes coarsely punctured, glabrous; male with pilose area at middle of Sternum 2+3, connected posteriorly to transverse band of pollinosity extending across sternum near posterior margin; female with Sternum 2+3 without anterior pollinose area, with transverse band widely interrupted at midline; Sternum 4, 5 in both sexes each with transverse pollinose band and with row of punctures close to posterior margin; Sternum 6 with some coarse punctures in middle anteriorly, and with pollinose band paralleling curved posterior edge, connecting to transverse band paralleling anterior margin, latter interrupted in middle; both sexes with lateral pit on Sternum 4, female with shallower additional pits on Sternum 5; male with ventral tooth on anterior femur; middle, hind calcars both small, acute.

Discussion. This species is easily distinguished by the presence of one temporal seta. *P. elegans* Grouvelle of Borneo and Sumatra lacks a temporal seta, while *P. silus* Bell and Bell of Mindanao, has 4 or 5. The type locality is on the Northern Peninsula of Sulawesi.

Omoglymmius (s. str.) *repetitus* Bell and Bell

Omoglymmius (*s. str.*) *repetitus* Bell and Bell, 1982:222.

For a complete description and illustrations, see the original description. This is the only species from Sulawesi which has a postorbital tubercle. The near absence of punctures on the pronotal carinae separates it from all species except *O. seriatus*. The closest relatives are *O. quadraticollis* (Arrow) of the Tanimbar Islands, and several species from New Guinea.

Two additional specimens were collected during Project Wallace, both females, labelled respectively "Sulawesi Utara, Dumoga-Bone N.P., 21 October, 1985, nr. base of Gunung Poniki, under bark of dead tree, Project Wallace, BM 1985-10," and "Sulawesi Utara, Dumoga-Bone N.P., 10 March 1985, on or under bark, Project Wallace 1985-10." (BMNH). The lengths of the three known specimens range from 6.0–7.4 mm. The known localities are on the Northern Peninsula.

Omoglymmius (s. str.) ferrugatus, new species

Type material. Holotype male (Figs. 3, 4), "Banggai Arch., Potil Kecil, 1°28′S, 123°34′E, 12–19, ii, 1980, M. J. D. Brendell, B. M. 1980-280, under bark of fallen tree" (BMNH).

Description. Length 7.0 mm. First segment of antenna scarcely swollen at base of principal tactile seta; antennal segments 1–10 punctate, punctures of distal segments more finely so; Segment 11 impunctate; head longer than wide; median lobe lance-shaped, its apex obtuse; frontal space broad, U-shaped; medial angle obtusely rounded, separated; posteriomedial margin slightly curved; occipital angle completely rounded; antennal lobe microsculptured, raised above level of temporal lobe; anterior end of temporal lobe extensively pollinose; pollinosity of orbital groove extended posterior to eye; temporal lobe with about 20 rather fine punctures; one temporal seta; postorbital, suborbital tubercles absent; eye large, round.

Pronotum short, subquadrate; length/greatest width 1.17; widest at middle, lateral margins only slightly curved; lateral margin scarcely emarginate anterior to hind angle; inner carina wider than outer one at middle of length; inner carina constricted just anterior to base; latter truncate; outer carina with about 30 very fine punctures; inner carina with 11–14 very fine punctures; pronotum without setae; prosternum without precoxal carina.

Elytra narrow, elongate; striae impressed, coarsely punctate; Interval 5 slightly more elevated than others; base of Stria 4 forming longitudinal scarp; pollinose area on base opposite Interval 3; Stria 4 with 1 seta at apex; apical striole with 1 seta; Stria 7 with about 7 setae near apex; metasternum densely but shallowly punctate; abdominal sterna finely punctate, punctures shallow, finely pollinose except near margins of Sterna 5, 6, where punctures coalesce into extensive pollinose areas; male with deep triangular lateral pit on Sternum 4 (female unknown); male with prominent ventral tooth on anterior femur; middle calcar minute, triangular; hind calcar triangular, its apex obtuse, its proximal margin sinuate.

Discussion. This species is obviously closely related to *O. wittmeri* Bell and Bell, 1982 and *O. continuus* Bell and Bell, 1982, both from the Sula Islands, which are about 100 km east of the Banggai Archipelago. In the key in Bell and Bell (1982) it will trace to Couplet 9, along with the two species from Sula. It will not go into either alternative, differing from *O. wittmeri* in the more quadrate shape of the pronotum, and the rounder medial angle, and from *O. continuus* in the uninflated first antennal segment, the presence of only 1 temporal seta, and the sharp medial edge to the antennal lobe. It differs from both species in the shape of the hind calcar.

Omoglymmius (s. str.) wallacei, new species

Type material. Holotype male (Figs. 5, 6), labelled "Indonesia: Sulawesi Utara, Gng. Ambang F. R., nr. Kotamobagu, 25 January 1985, lower montane forest, 1200–1400 m, fallen tree, Project Wallace B.M. 1985-10." Six paratypes. One female same as holotype; others same locality as holotype but one female, 18 February 1985; one female, September–October 1985, malaise trap: three males, 17 February 1985 (all BMNH).

Description. Length 6.7–8.3 mm; antennal segments 1–3 coarsely punctate, remaining segments more finely so; head about 1.5 times longer than wide; preocular portion produced; median lobe narrow, sides almost parallel, tip obtuse; anterior half of median lobe with 1–6 coarse punctures or impunctate; frontal space relatively small, U-shaped; medial angles obtuse, separated; temporal lobe evenly rounded posteriorly; anterior part of temporal lobe depressed, pollinose; orbital groove obsolete; posterolateral half of temporal lobe punctate; one temporal seta; postorbital, suborbital tubercles absent; eye large.

Pronotum relatively short; length/greatest width 1.12, widest slightly anterior to middle, sides curved, both base and apex narrowed; lateral margin sinuate anterior to hind angle; carinae subequal at middle; medial margin of lateral carina distinctly sinuate near base; outer carina widest at anterior 0.3; inner carina widest posterior to middle; outer carina coarsely, densely punctate; inner one with 4–8 coarse punctures; pronotum with setae or precoxal carinae; anterior part of prosternum, propleuron heavily microsculptured; prosternal process coarsely punctate; pronotal epipleuron coarsely punctate.

Elytra relatively short; striae coarsely punctate; base of Stria 4 with or without pollinose spot but without scarp, Stria 4, apical striole apparently without setae; Stria 7 with about 3 setae near apex; metasternum coarsely punctate along all margins, central disc finely punctate or nearly impunctate; abdominal sterna rather coarsely punctate, punctures of Sterna 3, 4 forming rather narrow band, but not uniseriate; lateral punctures of Sterna 3–5 enlarged, partly coalescent; punctures of Sternum 5 in broader band; those of Sternum 6 scattered; both sexes with deep, semicircular lateral pit on Sterum 4; male with ventral tooth on anterior femur; middle calcar small, acute; hind calcar with base occupying 0.25 of length of tibia, apex of calcar separated from tip of tibia by distance about equal to tibial spur, apex rounded, margin sinuate proximad to it.

Discussion. This species seems closest to *O. nasalis* Bell and Bell, of Buru, in the Moluccas, which it resembles in the depression of the anterior part of the temporal lobe, the microsculpture of the prosternum and propleuron, and the shape and punctuation of the pronotum. The less elongate snout might give trouble in our "Key to Species from Wallacea," as it will not give a clear alternative in Couplet 3. From *O. nasalis,* the first choice, it differs in the shorter snout, and the coarsely punctate pronotal epipleuron.

If it is taken to 3′, it traces to *O. wittmeri* Bell and Bell. It differs from the latter species in the longer head, coarser pronotal punctures, punctate median lobe and pronotal epipleuron and lack of a scarp at the base of Stria 4.

It is appropriate to name this species for Alfred Russel Wallace, the pioneer natural selectionist and entomological explorer of this region. The name also commemorates Project Wallace, which gathered the specimens used in this study.

Omoglymmius (s. str.) brendelli, new species

Type material. Holotype female (Figs. 7, 8), "Sulawesi Tengah, nr. Morowali, Ranu Lakes, 7–10, iii, 1980. M. J. D. Brendell, B.M. 1980-280, in rotten log" (BMNH). The locality is at 1°52′S, 121°30′E, near the eastern shore of the central part of Sulawesi, near the Gulf of Tolo.

Description. Length 5.7 mm; antennal segments 1–2 coarsely punctate, segments 5–10 finely punctate; median lobe broad, oval, coarsely punctate; frontal grooves narrow; frontal space small, U-shaped, its lateral margins broadly curved; medial angles rectangular, contiguous; posteriolateral margin oblique; posterior angle rounded, orbital groove fine, not extended posterior to eye; temporal lobe with 10–18 punctures on posterior, lateral portions; 1 temporal seta; postorbital, suborbital tubercles absent; eye large, round.

Pronotum moderately elongate, widest anterior to middle, length/greatest width 1.18; base, apex narrowed, lateral margins curved; lateral margin scarcely sinuate anterior to hind angle; inner carina slightly broader than outer one at middle; outer

carina widest at anterior 0.33; inner carina widest at posterior 0.33; base of inner carina slightly broadened, truncate; outer carina with 12–16 rather coarse punctures, inner carina with 1 minute puncture in anterior 0.25; pronotum without setae; precoxal carina absent; prosternum coarsely punctate; propleuron, anterior margin of prosternum pollinose; epileuron of pronotum punctate.

Elytron relatively long, narrow; stria impressed, coarsely punctate, punctures near apex smaller; base of Stria 4 without scarp or pollinosity; Stria 4 with 2 setae near apex; apical striole with 1 seta; Stria 7 with about 5 setae near apex, metasternum punctate; abdominal sterna with coarse, scattered punctures; female with round lateral pits on Sternum 4 (male unknown).

Discussion. This species will not key in the "Key to the Species of Wallacea" (Bell and Bell, 1982). It would reach Couplet 10, where the curved pronotal margins would suggest *O. viduus,* of the Kei Islands, but the reduced punctures of the pronotum would exclude it. The new species seems more like numerous species from the Greater Sundas and the Philippines, particularly *O. nemoralis* Bell and Bell from Sarawak, although the latter has more elytral setae. Unlike other *Omoglymmius s. str.* of Sulawesi, its affinities appear to be with the west and north.

We name this species for the collector, M. J. D. Brendell, who first suggested the possibility of working on the Rhysodini of Project Wallace.

Omoglymmius (s. str.) seriatus, new species

Type material. Holotype female (Figs. 9, 10), "Sulawesi Tengah, Mt. Tambusisi 4,000 ft, 1°39'S–121°21'E, 3–13 IV, 1980. M. J. D. Brendell, B.M. 1980-280, under bark of fallen tree" (BMNH). The locality is near the north coast of the central part of Sulawesi, just south of the Gulf of Tomini.

Description. Length 6.0 mm; antennal segments 1–2 coarsely punctate, outer segments successively more finely, indistinctly punctate; except for 10–11, latter impunctate; head elongate, nearly 2 times longer than wide; preocular portion produced; lateral surface near antennal base sloped dorsomedially; median lobe broad, rhomboidal, impunctate; frontal space small, U-shaped; medial angles slightly obtuse, slightly separated; posteriomedial margin oblique; temporal seta absent; temporal lobe with a few minute punctures in line above eye; eye large, round; mentum elongate, not depressed posteriorly.

Pronotum moderately elongate, length/greatest width 1.27, subquadrate, sides only slightly curved; widest anterior to middle; base slightly narrowed, apex more distinctly so; lateral margin of inner carina gradually sloped into paramedian groove, as in *Rhyzodiastes (Temoana)*; median groove very narrow, linear at middle; anterior and posterior median pits thus conspicuous; outer carina widest opposite anterior median pit, gradually narrowed posteriorly, its medial margin sinuate opposite basal impression; inner carina widest at middle, constricted between posterior median pit and basal impression, dilated, truncate at extreme base; carinae impunctate; pronotum without setae; prosternum with line of coarse punctures along anterior margin and anterior to coxae.

Elytra inconspicuously opalescent, moderately elongate; striae impressed, punctate; base without pollinosity; base of Stria 4 without scarp; Stria 4 with 1 seta near apex; Stria 7 with 4–5 setae near apex; metasternum with row of punctures along each margin, disc impunctate except for a few fine punctures in posterior part of median line; abdominal Sterna 3, 4 with punctures uniseriate; Sterna 5, 6 with punctures

scattered; Sternum 4 of female with deep, oval lateral pit; male unknown. Hind wings fully developed.

Discussion. The gradual slope of the lateral margin of the inner carina, the elongate snout, the narrow frontal grooves, and lack of pronotal punctures give this species much the appearance of a *Nitiglymmius.* The fully developed eyes and hind wings exclude it, as currently defined. It might, however, prove to be related to the latter subgenus when genitalia and other additional features have been studied. In the key to species from Wallacea (Bell and Bell, 1982), it would key to *O.* (s. str.) *nasalis* Bell and Bell, from which it is easily separated by the impunctate pronotum and narrow frontal grooves.

Omoglymmius (Indoglymmius) astraea, new species

Type material. Holotype male (Figs. 11, 12), "Gunung Muajat, 1,780 m, Sulawesi Utara, 6-10-85, R. W. Hornabrook" (NMNZ). The locality is on the Northern Peninsula. Paratypes, two females, one same data as male (NMNZ); the other from the same place, but dated 5-10-85 (NMNZ).

Description. Length 5.9–6.3 mm. Form elongate; antennae without basal setae or punctures; neither dorsal nor ventral surface at all opalescent; head elongate, margin sinuate anterior to eye; snout unusually broad; median lobe broad, rhomboid; frontal grooves narrow, linear; medial margin translucent along frontal space; frontal space very narrowly V-shaped; orbital groove absent; medial and temporal lobes impunctate; temporal setae absent; eye virtually absent, evident only under strong light as slightly less pigmented area, but not represented in external structure; postorbital tubercle absent; mentum impunctate; median tooth of mentum more prominent than in related species; base of mentum not pollinose, but with 2 pairs of deep pits.

Pronotum elongate, length/greatest width 1.38; sides evenly curved, not sinuate near hind angle; paramedian groove linear; median groove deep, linear; anterior, posterior pits large, deep; carinae entirely impunctate; marginal grooves narrow, deep, complete; prothorax without anterior "collar"; prosternum with a group of coarse punctures just anterior to coxae; epipleurae impunctate.

Elytra moderately elongate, less parallel-sided than in *O. semioculatus*; elytron with trace of longitudinal scarp at base of Stria 4; humeral tubercle lobate; elytra evenly convex in lateral view, not forming posterior "hump"; elytral striae shallowly impressed, coarsely punctate; elytra entirely without setae; metasternum impunctate except for 1–3 coarse punctures near lateral margins; abdominal Sterna 3, 4, 5 each with single transverse row of very coarse punctures; Sternum 6 with similar row near base, also curved transverse groove near apex; abdominal setae entirely absent; both sexes with ventral tooth on anterior femur, that of female small; male with calcars minute; female with small denticle posterior to tibial spur (simulating a second spur); female with distinct glabrous lateral pit in Sternum 4 and much smaller one on Sternum 5.

Discussion. This species has the most reduced eyes of any Rhysodine so far discovered. The elongate head, the very reduced eyes, and the shape of the pronotum suggest *O. (Nitiglymmius) semioculatus,* from Siargao, near Mindanao. The translucent area on the temporal lobe makes it trace to *O. (Indoglymmius) lineatus* (Grouvelle), but the latter species has well developed eyes and broad paramedian grooves. Whether the two are really related is doubtful, but a decision must await further studies.

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REVIEW OF THE GENUS *THAMIARAEA* THOMSON
IN NORTH AMERICA
(COLEOPTERA: STAPHYLINIDAE: ALEOCHARINAE)
WITH DESCRIPTION OF A NEW SPECIES

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Abstract.—*Thamiaraea americana* Bernhauer, an athetine aleocharine staphylinid rarely encountered in North American collections, is redescribed; illustrations of structural features are provided; and lectotype and paralectotype designations are made. *Thamiaraea lira* is described as new from Pennsylvania. Male members of North American *Thamiaraea* are distinctive due to a setiferous sex patch on the dorsum of the head and the structural modifications of the eighth tergite.

Thamiaraea Thomson, a primarily tropical genus of athetine staphylinids, includes about 60 described species worldwide. Nearly two-thirds of the described species are found in the Old World, with 6 from the Palearctic, 5 from the Ethiopian, 29 from the Oriental, and 10 from the Australian region. In the Americas, 3 described species are found in Argentina and Colombia, 3 in Guatemala and Panama, and 1 in North America. Palm (1972) and Lohse (1974) provided keys to the European forms, while Cameron (1939) described many new species from India and gave a key to these and to previously described species from the Indian subcontinent.

Thamiaraea and seven other genera were classified in the Schistogeniae by Bernhauer and Scheerpeltz (1926), a subtribe of the Myrmedoniini, based on the possession of 2-segmented labial palpi. Seevers (1978) was unconvinced of the phylogenetic significance of this subtribe and instead placed *Thamiaraea* and *Earota* Mulsant & Rey in the "*Thamiaraea* group" of the tribe Athetini, distinguished by the "relatively broad intercoxal processes, and the distinctive eighth male tergite."

The genus *Thamiaraea,* although very similar to other athetine genera in external habitus, can be distinguished from these by combination of 4,5,5 tarsal formula; first and second segments of labial palpus usually, but not always, fused (Figs. 5, 6); third segment of labial palpus narrowed at base, but distinctly dilated along mesal margin to apex (Figs. 5, 6); numerous sensilla along mesal margin of last labial segment; medial setae of prementum approximate at base; fourth segment of maxillary palpus at least ½ as long as preceding segment; temples margined below by fine ridge; mesosternal process usually reaching middle of coxae, separated from metasternal projection by short intercoxal isthmus (Fig. 8); distinctive male eighth tergite; and dorsum of male head (all North American species) with setiferous sex patch (Figs. 11, 12).

While providing identifications for specimens of aleocharine staphylinids submitted by D. L. Stephan (North Carolina State University), 2 male *Thamiaraea americana* Bernhauer were identified and confirmed by comparison with the type series. The original description given by Bernhauer (1907:401) is of little use in distinguishing

the species. During a recent examination of unidentified Aleocharinae in the Cornell University Insect Collection, I discovered a series of specimens of *Thamiaraea* from Pennsylvania. A detailed study of these specimens revealed morphological characters significantly different from the previously described species in North America (*T. americana*) and necessitated the description of a new species.

Since no study of the genus has ever been undertaken in North America, the purpose of this paper is to redescribe and illustrate *Thamiaraea americana* Bernhauer, to designate a lectotype from the syntype series in the Bernhauer collection, and to describe a new species from Pennsylvania. Recent comparative studies by Sawada (1970, 1972) have demonstrated the significance of structural characters in the mouthparts of aleocharines. In light of the emphasis placed on these character systems, I have described and illustrated the mouthparts of *Thamiaraea americana*. Most of the mouthpart characters discussed in the redescription (below) are probably genus-specific characters rather than species-specific characters.

Thamiaraea americana Bernhauer
Figs. 1–10, 15–19

Thamiaraea americana Bernhauer, 1907:401 (Type locality, Opelousas, Louisiana). Lectotype examined, designated herein.

Diagnosis. Adults of *T. americana* can be easily distinguished from those of the only other North American representative of the genus, *T. lira* n. sp. (described herein), by the apical margin of the male eighth tergite with a robust, outer tooth on each side, and a pair of short, truncate lobes at the middle (Fig. 15); by 2 small, blunt tubercles, 1 on each side of midline at middle of male eighth tergite (Fig. 15); by the elongate, rounded apical lobe of the paramerite with setal arrangement as in Figure 19; and by the characteristic female spermatheca (Fig. 18).

Redescription. Moderate sized, ranging in length from 3.1 to 3.6 mm. Body shape elongate, slender, somewhat flattened. Body color uniformly reddish brown to dark brown, except apical three abdominal segments which are darker. Antennae, legs and mouthparts paler, brownish yellow. Head, pronotum and elytra with reticulate microsculpture (polygonal pattern of microlines as in Fig. 13); abdominal terga with transverse microsculpture (interconnecting, wavy transverse microlines, Fig. 14). Integument surface covered with uniform vestiture of short, fine, densely arranged pubescence of microsetae; surface between punctures slightly shining; macrosetae present, but inconspicuous; punctures very fine, uniformly distributed.

Head broad across eyes (Ratio L/W = 0.80), basal angles broadly rounded, neck absent. Eye moderate in size, very finely pubescent. Temples moderately short, less than ½ length of eye, broadly rounded. Surface with microsculpture of polygonal pattern of microlines. Dorsal pubescence of microsetae directed mesad. Antenna moderate in length, reaching base of elytra; segments I–III somewhat elongate, with long, erect setae; segments IV–XI with vestiture of fine, recumbent pubescence and long setae; segment III slightly longer than II; segment IV quadrate; segments V–X transverse, progressively decreasing in length; segment XI slightly longer than IX and X combined, tapered and pointed apically. Labrum (Fig. 1) broadly transverse, slightly emarginate along anterior margin; outer angles broadly rounded; arrangement and number of labral macrosetae as in Figure 1; anterior margin at middle with
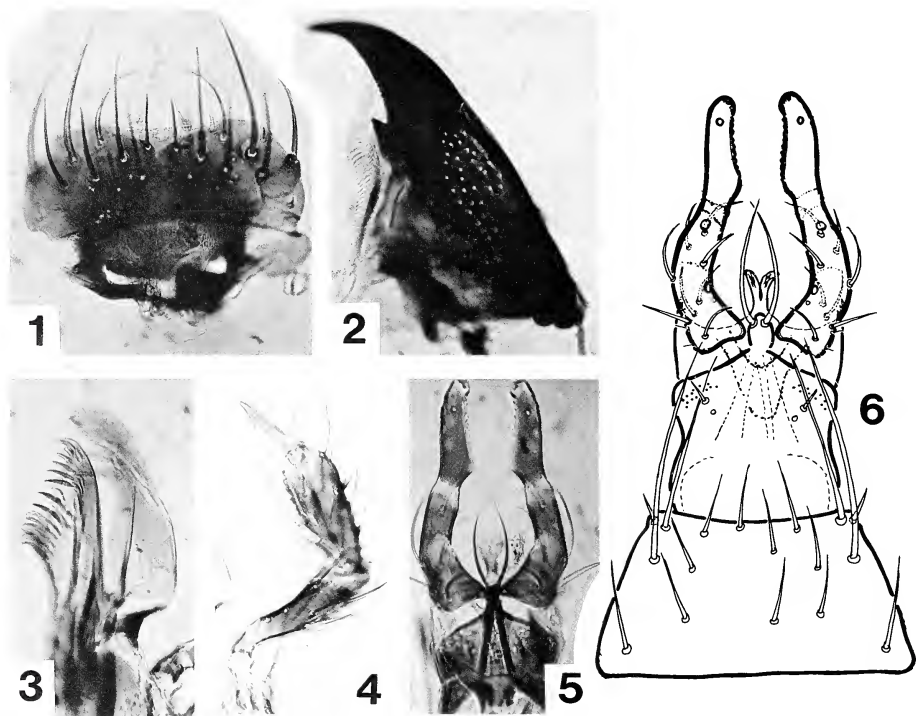
Figs. 1–6.   *Thamiaraea americana* Bernhauer. 1. Labrum. 2. Right mandible. 3. Galea and lacinia of maxilla. 4. Maxillary palpus. 5. Labium. 6. Line drawing of labium.

minute sensilla. Mandibles moderate sized, heavily sclerotized, curved and pointed at apex; right mandible (Fig. 2) with sharp, molar tooth near middle and with scrobal pore at distal end of lateral scrobe; left mandible without tooth, simple; narrow membraneous prostheca extending from base to near apex of mandible, finely ciliated at ends, but broader and more coarse at middle. Galea and lacinia of maxilla as in Figure 3; galea slightly longer and broader than lacinia, distal lobe finely and densely ciliate. Lacinia elongate, hooked and pointed at apex; mesal margin with 8 closely arranged, elongate spines at apex, with patch of fine setae with hooked apices below spines. Palpus of maxilla (Fig. 4) 4-segmented; segment I small; segment II elongate, slightly expanded towards apex; segment III as long as segment II, but more incrassate at apex; segment IV at least ½ as long as segment III, subulate. Bundle of filamentous sensilla present at base of segment IV. Mentum of labium (Fig. 6) transverse, trapezoidal, slightly emarginate along anterior margin; arrangement and number of macrosetae as in Figure 6; 2 medial setae of prementum (Figs. 5, 6) long, convergent at apices, approximate at base. Labial palpi (Figs. 5, 6) elongate, appearing 2-segmented (segment I and II usually, but not necessarily, fused); segment I + II curved and convex laterally; segment III shorter and narrower than segment I + II, somewhat dilated on mesal margin; length of mesal margin with numerous sensilla; arrangement

Figs. 7–10. *Thamiaraea americana* Bernhauer and North American distribution of *Thamiaraea* spp. 7. Pronotal pubescence pattern, *T. americana*. 8. Mesosternal process, metasternal projection and intercoxal isthmus, *T. americana*. 9. Known distribution of *T. americana* (closed circles) and *T. lira* n. sp. (closed triangle). 10. Pubescence pattern of right elytron, *T. americana*.

and number of palpal macrosetae as in Figure 6. Ligula long, deeply bifid, lobes divergent.

Pronotum flattened, broadly transverse (Ratio L/W = 0.70), with surface microsculpture of polygonal pattern of microlines; surface dull to slightly shining; pubescence of microsetae dense, uniform, in a narrow median strip directed caudad or laterocaudad, with remaining microsetae swirling laterad from median row (Fig. 7 = Pattern C of Seevers, 1978, or Type IV of Lohse, 1974); punctures fine, uniform, inconspicuous. Mesosternal process moderately long, attaining middle of mesocoxal cavities, broadly rounded at apex, separated from narrowly rounded metasternal projection by a short, raised intercoxal isthmus (Fig. 8). M:i:m ratio (mesosternal process: isthmus: metasternal projection) = 7.6:1:5.9.

Elytra slightly wider at base than maximum width of pronotum; microsculpture of polygonal pattern of microlines; integument shining; pubescence of microsetae extremely dense, moderately short, appressed, in slightly sinuate pattern, directed caudad or laterocaudad (Fig. 10 = Pattern S of Seevers, 1978); punctures fine, uniform, and inconspicuous.

Abdominal terga III–V with shallow, basal impressions, impunctate; tergal surfaces with faint microsculpture of wavy, transverse microlines; pubescence of microsetae sparse, more dense on basal 3 terga; punctures very fine, slightly asperate. Apical margin of terga III–VI with row of long setae. Tergal integument slightly shining.

Male. Median lobe of aedeagus as in Figure 17. Apical lobe of paramerite (Fig. 19) elongate, broadly rounded apically, with 2 short, apical setae; 1 erect seta on outer surface; and 1 long, curved seta on inner surface.

Female. Spermatheca as in Figure 18.

Secondary sexual characteristics. Apical margin of tergum VIII of male (Fig. 15) with a strong, robust tooth on each side; a pair of short, but slightly protruding truncate lobes at middle; and a pair of small, blunt tubercles, one on each side of midline, near middle of tergite. Sternum VIII unmodified, uniformly rounded. Tergum VIII of female with apical margin broadly emarginate (Fig. 16); sternum VIII unmodified, uniformly rounded. Head of male with a setiferous sex patch on frons, consisting of a brush of caudally-directed setae which are more prominent than the other setae of the head (Figs. 11, 12). This setal brush is within a glabrous area which is also defined by a cuticular impression or pit. An undoubted parallel development of setiferous patches is found on the heads of male beetles of the staphylinid genus *Neobisnius* (see Frank, 1981; Faustini and Halstead, 1982).

Distribution. The species is presently known from Louisiana and North Carolina (Fig. 9).

Material examined. 3 males, 1 female. UNITED STATES: *North Carolina*: Orange Co., Chapel Hill, 27-VI-1986, Ms. C. S. Rosenberg (2 males) CUIC. *Louisiana*: Opelousas, May (1 male, 1 female) FMNH.

Type designation. In the original description of *T. americana* (Deutsch. Entomol. Z., 1907:401), Bernhauer listed Opelousas, Louisiana, as the type locality, but did not mention the number of specimens examined. One male and one female specimen are present in the Bernhauer collection in the Field Museum of Natural History (Chicago). The male is hereby designated as the lectotype; it is labelled: Opelousas, Louisiana May (label cut in two)/"Klages"/"140"/"americana Brh. Typus"/Chicago NHMus, M. Bernhauer Collection. I have added the label: LECTOTYPE *Thamiaraea americana* Bernhauer, desig. E. R. Hoebeke 1986. The male genitalia, and terminal terga and sterna have been dissected and mounted in Euparol on a micro-coverslip (6 mm diam.) and placed below the specimen. The female, herein designated paralectotype, bears the same data as the lectotype, except for the labels "120" and "americana Brh. Cotypus." I have added the label: PARALECTOTYPE *Thamiaraea americana* Bernhauer, desig. E. R. Hoebeke 1986. The terminal terga and sterna, and spermatheca have been dissected and mounted in Euparol on a micro-coverslip and placed below the specimen.

Biological notes. Several Indian species of *Thamiaraea* are recorded from the fungus *Polyporus* (Cameron, 1939), and the common British species (*T. cinnamomea* and *T. hospita*) have been reported "at the exuding sap of trees burrowed by the larvae
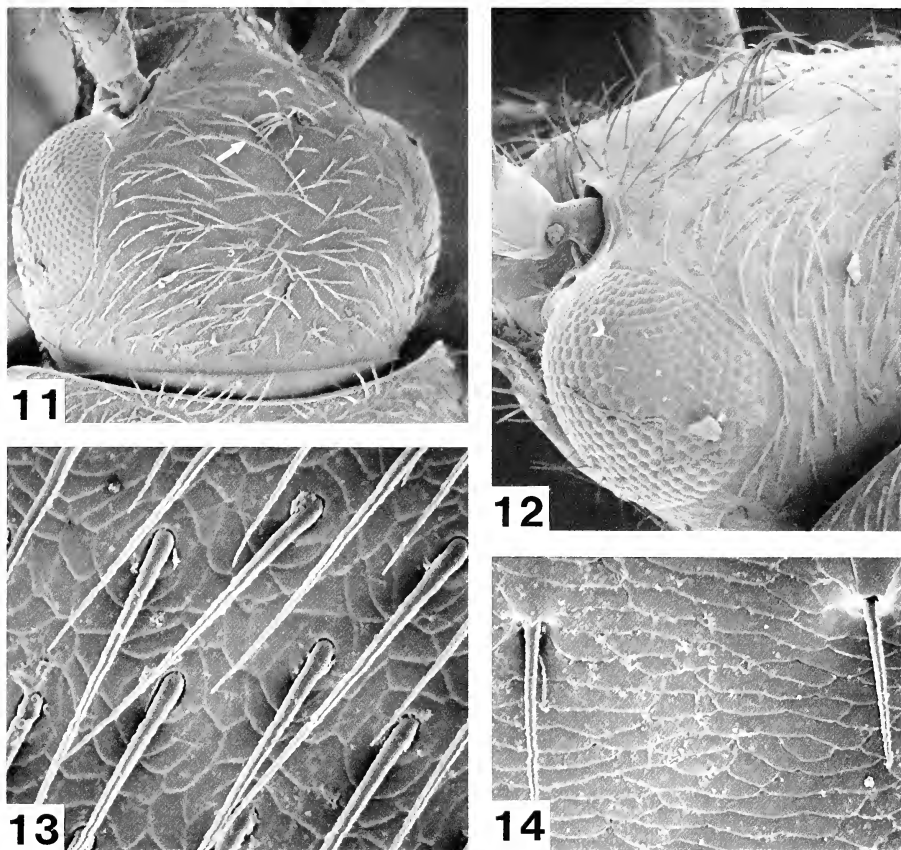
Figs. 11–14. *Thamiaraea lira,* new species. 11. Male head, dorsal aspect, sex patch marked by arrow. 12. Male head, lateral dorsal aspect, sex patch marked by arrow. 13. Microsculpture of pronotum. 14. Microsculpture of tergum VIII.

of the moth *Cossus ligniperda.*" (Joy, 1932:50) and in rotting fungi (Benick, 1952: 107). The North Carolina specimens were found "associated with slime flux on [a] trunk of *Quercus alba* L.," agreeing with the habits of the British species.

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Thamiaraea lira, new species
Figs. 9, 11–14, 20–23

</div>

Diagnosis. The body shape, color, vestiture and microsculpture are similar to that of *T. americana,* but adults of *T. lira* n. sp. can be readily separated from those of the latter species by the apical margin of the male eighth tergite with a long, slender tooth on each side and a pair of protruding, rounded lobes at the middle (Fig. 20); by the deeply-channelled, broad ridge along the midline of the male eighth tergite (Fig. 20); by the short, truncate apical lobe of the paramerite with setal arrangement as in Figure 22; and by the shape of the female spermatheca (Fig. 23).
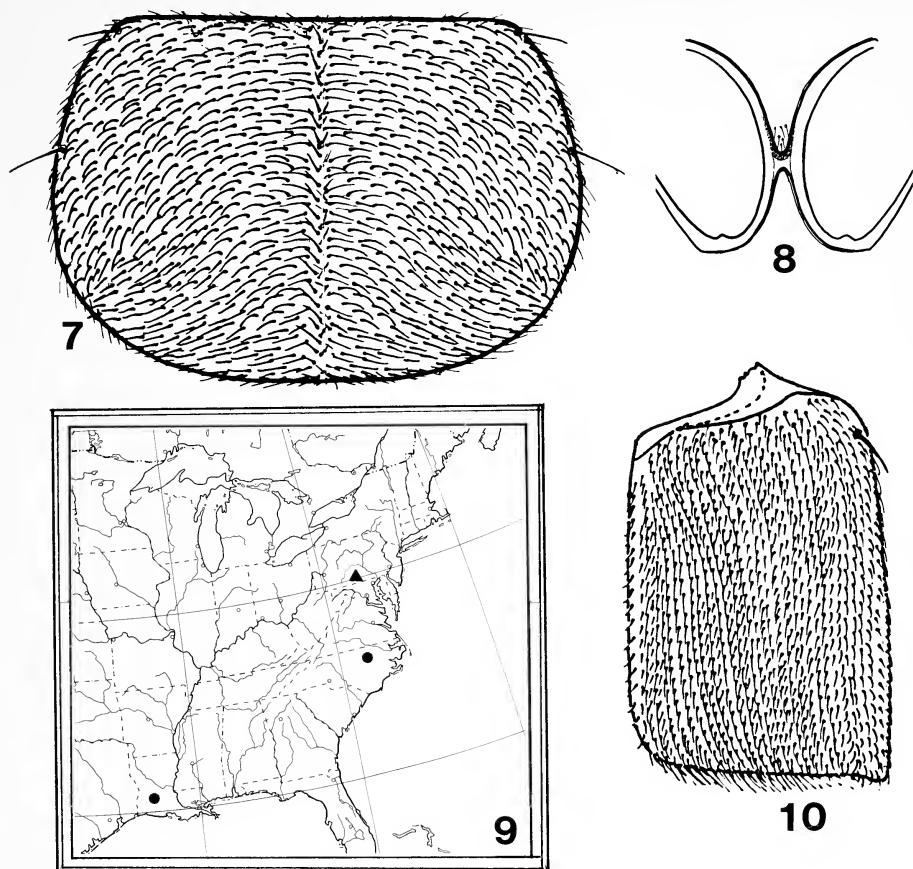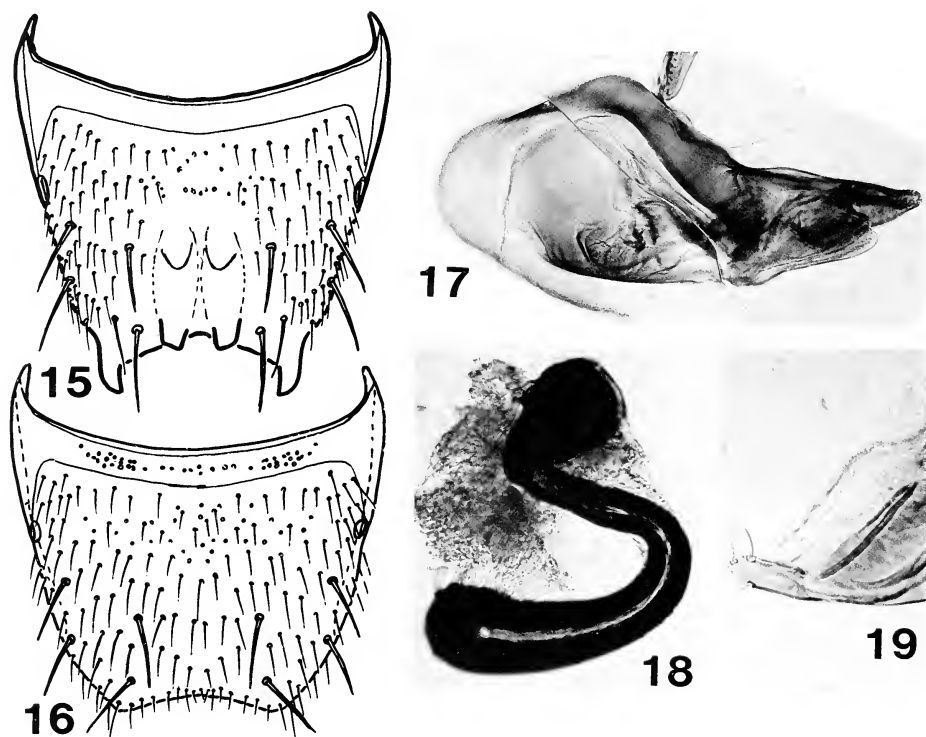
Figs. 15–19. *Thamiaraea americana* Bernhauer. 15. Male tergum VIII. 16. Female tergum VIII. 17. Median lobe of aedeagus, lateral aspect. 18. Spermatheca. 19. Apical lobe of paramerite.

Description. Length 3.2–3.5 mm. Body color reddish brown, with head, apical III–IV abdominal segments, and basal impressions of abdominal segments III–V dark brown. Antennae yellowish brown with distal segments slightly darker. Legs and mouthparts uniformly light yellowish brown.

Head broad across eyes (Ratio L/W = 0.78), basal angles broadly rounded, neck absent. Eyes prominent, scarcely pilose. Dorsal pubescence of microsetae moderately dense, appressed, directed medially. Microsculpture reticulate, forming polygonal pattern of microlines; surface shining between punctures; punctures very fine, uniformly distributed. Antenna moderate in length, extending to basal ⅓ of elytra; segments loosely organized; segment II shorter than I, somewhat broadened apically; segment III elongate, longer than II, attenuate basally, broadened at apex; segments I–III lacking fine recumbent pubescence; segment IV–X becoming progressively shorter, more transverse to segment XI; segment XI longer than IX and X combined, pointed apically.

Pronotum flattened, broadly transverse (Ratio L/W = 0.70); anterior margin truncate to slightly and broadly emarginate at base of head; posterior margin broadly arcuate at middle; slightly bisinuate towards outer angles; lateral margins broadly curved; surface with microsculpture of polygonal pattern of microlines (Fig. 13);
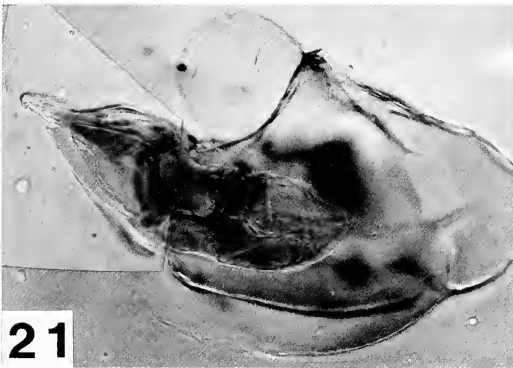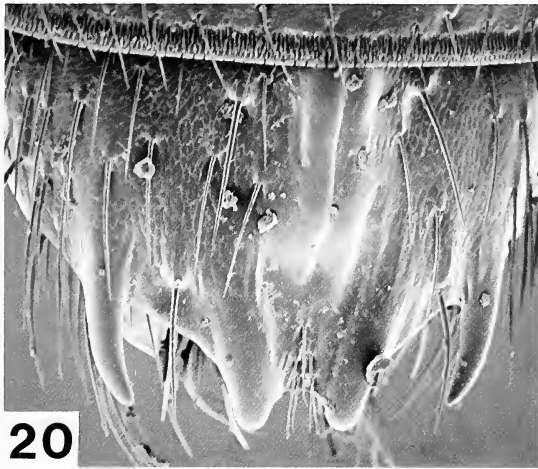
Figs. 20–23. *Thamiaraea lira,* new species. 20. Male tergum VIII. 21. Median lobe of aedeagus, lateral aspect. 22. Apical lobe of paramerite. 23. Spermatheca.

surface slightly shining to dull between punctures; pubescence of microsetae fine, dense, appressed; pubescence pattern consisting of narrow strip along midline with microsetae directed caudally, and remaining microsetae directed laterocaudally from midline and narrow band of microsetae along posterior margin directed laterally from midline; punctures fine, uniformly distributed.

Elytra slightly wider than pronotum at base; microsculpture of polygonal pattern of microlines; surface slightly shining between punctures; punctures fine, slightly asperate, uniformly distributed; pubescence of microsetae directed caudally, slightly sinuate.

Abdominal terga with moderate setae and punctures, with faint microsculpture of interconnecting, transverse microlines; terga III–V with broad, shallow transverse impression; impression without punctures; terga III–VI with row of long caudally directed setae along apical margins; surface between punctures smooth, shining; punctures moderate to sparse, somewhat coarse, uniformly distributed.

Male. Median lobe of aedeagus as in Figure 21. Apical lobe of paramerite (Fig. 22) short, robust, with truncate apex, and with 2 relatively short apical setae, and 2 long, erect setae arising from the outer surface; the bases of these setae are nearly approximate.

Female. Spermatheca as in Figure 23.

Secondary sexual characteristics. Apical margin of male tergum VIII (Fig. 20) with a long, slender tooth on each side; a pair of prominent, rounded lobes at the middle; and a broad, deeply-sulcate longitudinal ridge along the midline. Male head with brush of setae on frons (Figs. 11, 12). Apical margin of female tergum VIII similar to that of *T. americana,* but more truncate.

Distribution. Known only from the type locality, Arendtsville, Pennsylvania (Fig. 9).

Type material. Holotype, male, with the following labels: Arendtsville. Pennsylvania, 5-24-1927, S. W. Frost/HOLOTYPE *Thamiaraea lira* n. sp., desig. E. R. Hoebeke 1987. Allotype, female, with the labels: Arendtsville, Pennsylvania, 10 May 1927, S. W. Frost Coll./ALLOTYPE *Thamiaraea lira* n. sp., desig. E. R. Hoebeke 1987. The holotype and allotype are in the Cornell University Insect Collection.

Paratypes, 4 males, 1 female. Same data as type, except different dates. All paratypes are deposited in the Cornell University Insect Collection.

Etymology. The species epithet is derived from the Latin *lira,* meaning "earth or ridge thrown up by the plow, furrow slice," and refers to the broad, channeled ridge along the midline of the male eighth tergite (Fig. 20).

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FOSSIL CYDNIDAE (HETEROPTERA) FROM THE OLIGO-MIOCENE AMBER OF CHIAPAS, MEXICO

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Abstract.—The family Cydnidae (Heteroptera) is represented by 2 known specimens in fossil amber from Chiapas, Mexico. One is an immature which cannot be placed with certainty; the other is in the Amnestinae, *Amnestus guapinolinus,* new species. The specimens are approximately 24 million years old and are the first fossil Cydnidae reported from amber.

Fossil Heteroptera have been reported in the Mexican amber by Wygodzinsky (1959) in the Dipsocoridae, and by Hurd et al. (1962) in the Aradidae, Hebridae and Isometopidae. Neither cydnids nor other Pentatomoidea have been reported from Mexican amber. Larsson (1978) indicated that this family is absent from the Baltic amber as well, hence I believe that these are the first definite records of cydnids from fossiliferous amber, although Dolling (1981) mentions that he has seen a thaumastellid in Lebanese amber from the lower Cretaceous.

I have had the opportunity to acquire amber from the Simojovel region of Chiapas, and to examine the private holdings of persons dealing in the amber trade, most of which is destined to become jewelry. Durham and Hurd (1957) have dated the Simojovel amber deposits as upper Oligocene to lower Miocene, based on associated marine fossils. The Oligo-Miocene boundary is now estimated at 23.7 Ma (Berggren et al., 1985).

To date I have examined two specimens belonging to the family Cydnidae; one, an adult assignable to the subfamily Amnestinae and the other a 5th instar nymph, which is not assignable to any subfamily with certainty.

Amnestus guapinolinus, new species

Description. Elongate-oval (Fig. 1); length 1.6 mm, width 0.95 mm; color light brown, membrane of corium clear, transparent. Intramargin of juga each with five pegs; tylus slightly produced relative to juga and bearing four pegs at tip. Antennae appearing four segmented, as in other members of genus; pedicel divisions inconspicuous.

Pronotum with weak transverse impression; cervical margin deeply concave. Protibia with three short and two long lateral spurs on outer margin and two long spurs at apex; inner margin unarmed. Profemora with small, blunt, tubercle approx. one-third distance from apex on inner face (Fig. 2); meso- and metafemora unarmed.

Scutellum triangular, without apical lobe; slightly longer than wide. Hemelytra with claval commissure; apical margin of corium sinuate, though not as strongly sinuate as in *A. unidentatus*; embolar angle not prolonged as in that species.

Holotype. Female: Simojovel area, Chiapas, Mexico. Embedded in a cut and polished piece of fossil amber, polygonal in shape, measuring 3.4, 2.5 by 1.7 cm in
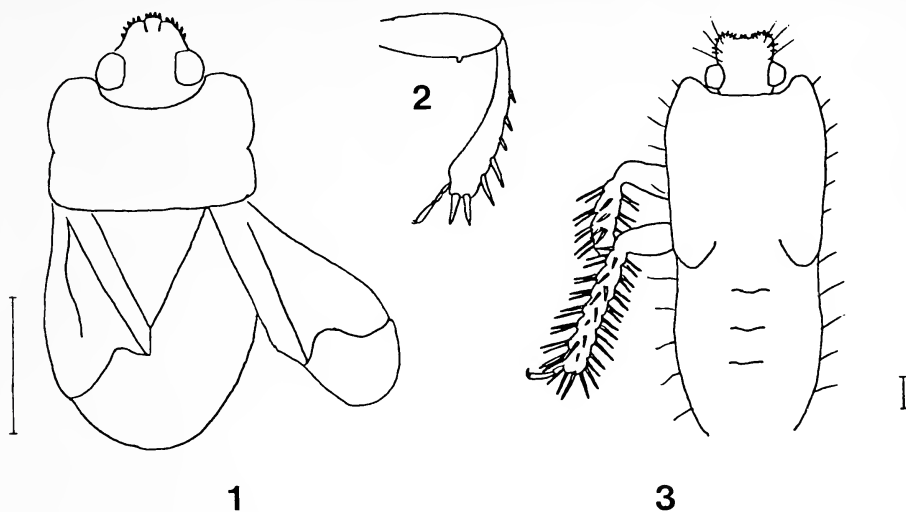
Figs. 1–3. 1, 2. *Amnestus quapinolinus* n. sp. 1. Dorsal view. 2. Anterior view, left, front leg. 3. Cydnidae, *incertae sedis,* dorsal view. Vertical bar = 0.5 mm.

dimension. Cat. No. CV-020. Private collection of Sr. Carlos Villar, Simojovel, Chiapas.

Remarks. This species is small, even for members of the genus *Amnestus,* which range in size from 1.6–4.5 mm. Froeschner (1960) provides a review of the genus. It is the only genus in the subfamily Amnestinae and is restricted to the western hemisphere. *Amnestus* can be recognized by the presence of 4 or 5 pegs on the tip of the tylus, but most importantly, by the presence of a claval commissure. This species differs from the extant species by the presence of a blunt, profemoral spur about one-third the distance from its apex. Some male *Amnestus* have a spine on the profemur, but this is medial to basal in position and is supposedly an important secondary sexual characteristic. Froeschner (1960) notes that there was confusion in the past with some earlier descriptors who thought it was the females that had the profemoral spines. The presence of a profemoral process in this female should not be accorded undue significance since metafemoral spines are found in the females of some species. *Amnestus quapinolinus* also is unique in having the scutellum longer than wide. In all extant *Amnestus* the scutellum is wider than long or subequal. In its small size, number of jugal pegs and slightly protruding tylus, it most closely resembles *A. brunneus* Signoret, a species which is known from Oaxaca.

Cydnidae, *incertae sedis*

This specimen is a 5th instar nymph (Fig. 3), 6.5 mm in length, which has undergone heterogenous distortion, a not uncommon feature of amber fossils, such that the body has become extremely dorso-ventrally compressed. Since the specimen was an immature, the wings, scutellum and metapleural evaporatorium are not available for analysis; and since it is these structures which have many of the most diagnostic

features, it cannot be assigned to any fossil or extant genus. Nevertheless, the following salient characters are evident. The tibiae are heavily bristled and all tarsi are present. The pronotal margins have six long, thickened setae on each side. The tylus and juga are subequal, the tip of the tylus has 2 pegs, each jugum has eight submarginal pegs and three long setae. In addition, the disc of each jugum has a long seta.

Froeschner lists five subfamilies of Cydnidae among the extant species. Dolling lists eight, but this includes three groups usually given family status, Thaumastellidae, Corimelaenidae and Thyreocoridae. Since this specimen has two pegs on the tylus, submarginal setae on the pronotum and all of its tarsi, it could be placed in the Cydninae. Cydninae are known from three genera from the Eocene of Colorado (Cockerell, 1909). However, the majority of fossil cydnids known from the North American Paleogene, including four genera from the Florissant shales, (Scudder, 1890), and *Paleofroeschnerius* from Tennessee (Schaefer and Crepet, 1986), have a distinctive, short, triangular scutellum. An elongate scutellum with an apical lobe, is the usual condition in the Cydninae. A short triangular scutellum is typical of the Amnestinae but, none of these genera seem to have the claval commissure that characterizes Amnestines. Popov (1986) has described a subfamily, Clavicorinae, from the Mesozoic of Mongolia which is characterized by a short, triangular scutellum and a claval commissure. They differ from the Amnestinae by their larger size. The Cenozoic genera could be considered to belong to an extinct subfamily, or they could represent forms intermediate between the Cydninae and the Amnestinae or Clavicorinae. Obviously, the immature status of the present specimen occludes its placement within, or its exclusion from, any of these schemes.

This specimen occurs in a piece of amber which originates from the Simojovel area of Chiapas and I am depositing it as a voucher for the Family Cydnidae from the Mexican Oligo-Miocene with the American Museum of Natural History. It has my specimen number DT-001.

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THE SPECIES OF *ENTEDON* IN AMERICA NORTH OF MEXICO (HYMENOPTERA: EULOPHIDAE)

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Abstract.—The species of the genus *Entedon* are revised for America north of Mexico. Eighteen species are recognized and a key is presented. Two species previously known from Europe (*methion* Walker and *stephanopachi* Heqvist) are present in North America as well as an additional species (*ergias* Walker) imported for biological control of smaller European elm bark beetle. Eight species are described as new (*ashmeadi, ernobii, genei, procerus, pecki, darleneae, teedoe,* and *anthonomi*). Lectotypes are designated for *Entedon bigeloviae* Ashmead, *E. occidentalis* Girault, *E. tachypterelli* Gahan, *Pleurotropis leucopus* Ashmead, and *Eriglyptus robustus* Crawford. Species of *Entedon* are primary parasites of a variety of beetles and one is known to attack Hymenoptera (Tenthredinidae). The known host species are indexed by family with their respective parasites.

Species in the genus *Entedon* are primary parasites of a variety of weevils, bruchids, bark beetles and other Coleoptera, with one species also attacking sawflys. The most recent North American Hymenoptera catalog (Burks, 1979) listed only 6 species from the Nearctic, with one species having been imported into the United States for the biological control of the smaller European elm bark beetle (*Scolytus multistriatus* (Marsham)). Aside from a short key by Girault (1922), the North American species have never been revised. It is apparent that there are undescribed species present, and that the limits of the previously known species are poorly defined. In addition, it has been discovered that some species known from Europe also occur in North America. This paper remedies these problems and also presents a key to the species found in North America.

The European species of *Entedon* have been revised for Britain (Graham, 1971) and Hungary (Erdös, 1944, 1951). Additional individual species have been described subsequent to these papers (e.g., Erdös, 1954; Boucek, 1974; Szelényi, 1977a, b). Unfortunately, no one has yet attempted to completely revise the Palearctic species for this genus and some gaps in our knowledge of that fauna remain.

Erdös (1944) proposed a number of subgenera within *Entedon*. Graham (1963, 1971) used a number of species groups, some of which corresponded to the subgenera of Erdös, while others consisted of various parts of those subgenera. The North American species will not fit either of these groupings and I believe that proposing further infrageneric groupings at this time would only further complicate the problem.

MATERIALS AND METHODS

The individual species are treated alphabetically after the key. Morphological terminology largely follows Graham (1959, 1963) and Gibson (1986). Terms for sculpture follows Harris (1979) and for common names of host species Werner (1982).

The metasoma includes the petiole (T1) so that T2 is the first gastral tergum. The funicular articles are numbered F1–3 in females and F1–5 in males and do not include the annelli. The term OCL refers to the distance from the posterior edge of a lateral ocellus to the occipital carina. Interscrobes refers to the area medially between and above the toruli which usually extends upwards to the junction of the frons and vertex. In most species it is indicated by a narrow smooth area interrupting the sculpturing of the frons. The frontal grooves (also called the arms of the frontal fork in Graham, 1959) extend outward from the middle of the face at an angle to dorsal edge of the eye. They form a v-shaped line, when present, and are very narrow and often difficult to see in females. They are absent in the majority of species and care should be taken when assessing this character.

The speculum is the area of the membrane of the forewing bounded by the lines of setae generally referred to as the cubital and basal veins. Since these setae are absent in most species of *Entedon,* the speculum is referred to as being open (closed when the setae are present, Fig. 25). I have referred to this character by the use of the presence or absence of the individual lines of setae. However, for clarity I have also included the corresponding condition of the speculum in parentheses.

The size of the individual alveoli on the midlobe of the mesoscutum is given in relative terms. This character is difficult to quantify and is subject to some variation. In specimens with larger alveoli, the distance between the sculptural ridges gives the appearance of a very shiny surface and even in species with moderate sized alveoli this shiny appearance remains. However, in some species these alveoli are small and close together and give the dorsum a dull appearance. Because of the subjective nature of this character and that fact that surface dirt may obscure the surface appearance, I have not used it in the key, but have only mentioned it in the species descriptions. All structures were measured at their longest or widest points.

The ratio of length to width of the metasoma is an often used character in this genus, but it is subject to considerable variation depending on the way in which it is preserved. Air-dried specimens always have the dorsum of the metasoma collapsed and in species in which the metasoma is 3 or 4 times as long as wide, the terminal segments tend to bend upwards. This distortion makes it difficult to obtain the exact ratio of length to width. As a result, the ratios given in the key are subject to some variation, but should not overlap those of the opposing part of the couplet. Thus, while the length to width of the metasoma of *E. ashmeadi* may vary slightly from exactly 2.0, it will not be anywhere close to the ratio of *E. teedoe.* Critical-point dried specimens generally do not suffer from these problems, but these are rare in collections.

Overall variation observed in specimens of new species is noted in the species descriptions, whereas for previously described species it is included under notes. In the key and in some of the diagnoses I have used a single estimate of length to width ratio, malar distance, and so on (e.g., couplet 4). These figures represent an approximate mean for that character and while there may be some variation around that estimate there will not be overlap.

Although this study is based primarily on North American material, I have studied specimens of most of the European species and consulted the available literature for that region. I have also examined species from other zoogeographic regions (e.g., Ethiopian and Oriental), but I have not attempted an exhaustive survey of those

species. As a result I have been able to include characters in the species descriptions which are known to vary in European species, even though none of the Nearctic species possess those features (e.g., the swollen marginal vein present in males of *E. costalis*).

Data on specimens examined is given in abbreviated form with the collector name omitted. The repository for specimens is indicated after each series or groups of series within a given state or province. Distribution data from the specimens examined is summarized under the distribution section. If the known distributional data is fragmentary, only the states or provinces are listed.

Acronyms for museums are given in the acknowledgments.

Entedon Dalman

Entedon Dalman, 1820:136,181.
    Type-species. *Entedon cyanellus* Dalman. Designated by Ashmead, 1904.
Pleuropachus Westwood, 1837:437.
    Type-species. *Entedon costalis* Dalman. Orig. Desig.
Pleuropachys Förster, 1856:78. Emendation.
Eriglyptus Crawford, 1907:179. Synonymy by Girault, 1916a.
    Type-species. *Eriglyptus robustus* Crawford. Orig. Desig.
Entedonella Girault, 1913:154. Synonymy by Girault, 1916a.
    Type-species. *Entedonella magnifica* Girault. Orig. Desig.
Metriocharis Silvestri, 1914:214. Synonymy by Boucek and Askew, 1968.
    Type-species. *Metriocharis viridis* Silvestri. Orig. Desig.
Nephelentedon Erdös, 1944:18 (as subgenus of *Entedon*).
    Type-species. *Entedon subfumatus* Erdös. Orig. Desig.
Megalentedon Erdös, 1944:27 (as subgenus of *Entedon*).
    Types-species. *Entedon thomsonianus* Erdös. Orig. Desig.
Dolichentedon Erdös, 1944:31 (as subgenus of *Entedon*).
    Type-species. *Entedon cioni* Thomson. Orig. Desig.
Chlorentedon Erdös, 1944:44 (as subgenus of *Entedon*).
    Type-species. *Entedon subovatus* Thomson. Orig. Desig.
Trochentedon Erdös, 1944:61 (as subgenus of *Entedon*).
    Type-species. *Entedon crassiscapus* Erdös. Orig. Desig.

Diagnosis. Species of *Entedon* can be separated from other Entedoninae by the following characters: female antenna with 3 annelli, 1st largest, 3 funiculars, and 2-segmented club (Figs. 26–42); mandibles with 2 teeth; pronotum reduced dorsally, expanded at lateral angles, without a transverse carina; notauli incomplete (Figs. 1, 2); propodeum with complete median longitudinal carina (Fig. 5), laterally with an inverted L-shaped sulcus anterior to and laterad of spiracle, tubercle present ventrally below the spiracle; second metasomal tergum (T2) with an oval membranous area adjacent to the petiolar emargination; stigmal vein petiolate; postmarginal vein about as long as stigmal (Figs. 23, 24); hind coxae triangular in cross section. In addition, the frontal grooves are generally absent, the petiole is reduced to a narrow transverse band dorsally (females), and the cubital and basal vein setae are absent at the base

of the wing (speculum open). However, one or all of these last 3 characters are known to occur in some species and should be checked against the species diagnoses.

Males are generally similar to the females, but differ consistently in some characteristics. The scape is generally broader relative to its width and has a long sensory strip along the anterior edge (Figs. 7, 8). The lengths of the flagellomeres are usually close to those of the females, except that the terminal two antennomeres are usually distinctly separated rather than fused and the setae on the segments are much denser. The interocular space is broader, so that in frontal view the eyes are wider apart and the overall width of the head is greater. The sculpturing of the interscrobal area and the face may differ, with the alveoli often larger and the smooth area more extensive. The frontal grooves, when present, and the occipital carina are often more strongly expressed than in the females. The metasoma is generally shorter relative to its width than in the females and may have an antero-medial light-colored spot. The petiole is usually at least as long as wide.

The monophyly of *Entedon* rests primarily on the structure of the median propodeum. None of the other genera which I consider to be closely related to *Entedon* possess a simple, complete, median carina situated in a narrow depressed area. Although the relationships of genera within the subfamily have not been critically assessed, a number of genera resemble *Entedon* in being strongly sclerotized (head and mesosoma not collapsing when dried), having strong alveolate sculpture on the head and mesosoma, and presence of a postero-lateral bump on the propodeum. This group includes the genera *Paracrias, Chrysocharis, Horismenus, Pediobius, Mestocharis, Derostenus,* and *Colpixys* (the last not known to occur in North America). *Mestocharis* has a median carina, but it is expanded anteriorly into a cup-shaped depression and lacks lateral depressions. Species of *Pediobius* have paired submedian carinae, and in *Horismenus* and *Paracrias* there is a broad, smooth, raised area bounded laterally by an equally broad, sunken, sculptured area. Species of *Colpixys* possess a broad sunken area medially and there is no median carina. The oval membranous area on the second metasomal tergum adjacent to the foramen is shared only with *Colpixys* and this character may indicate that these two genera are sister groups. I have also seen specimens that I would place as *Entedon* from Australia that have this oval area darkened and sclerotized rather than light colored and membranous. The postero-lateral expansions of the pronotum, which form a bump or protuberance, are not found in the same form in related genera. However, *Colpixys gigas* Boucek has a similar, although not as large, bump in this same area.

Another interesting character is the lack of scrobal grooves in species of *Entedon*. Almost all the other related genera (except *Derostenus*) possess distinct scrobal grooves which originate at the toruli and extend upwards to the frontal groove. Since the presence of scrobal grooves is almost certainly the primitive condition in entedonines, the lack of those grooves could be viewed as a synapomorphy for *Entedon*. Unfortunately, the lack of grooves in at least one other fairly closely related genus (*Derostenus,* which is not a likely sister group to *Entedon*) means that some independent loses of this character have occurred. In addition, several species of *Chrysocharis* and *Achrysocharoides* lack scrobal grooves and are similar in this respect to *Entedon*.

Entedon is a cosmopolitan genus which has been recorded from a number of hosts. The species are parasitic primarily on various families of Coleoptera, particularly Anobiidae, Bostrychidae, Buprestidae, Cerambycidae, Curculionidae, Mordellidae,

and Scolytidae (Boucek and Askew, 1968). There are also a number of records from hosts in the Lepidoptera, Diptera, and Hymenoptera which have been considered doubtful. It is now confirmed that one species parasitizes stem-gall forming tenthredinid sawflys.

This key will not always work for males, although some of them will run through with the characters common to both sexes (e.g., *occidentalis* and *darleneae*). However, since males remain unknown for several of the species, the construction of a separate key for males would be of limited value at this time. I have noted useful male characters where possible in the key and additional information is given, where available, in the species descriptions and diagnoses.

KEY TO FEMALES OF NORTH AMERICAN *ENTEDON*

1. Mandibles enlarged, with ventral tooth longer than dorsal (Fig. 3); oral fossa at least 4.0× malar space; clypeus protruding forward over mouthparts; foretibia with curved spine on anterior surface (Fig. 4) 2
– Mandibles with teeth subequal in length (Fig. 9); oral fossa 3× as broad as malar space or less; clypeus truncate; foretibia without curved spine on anterior surface .. 3
2. Foretibia with a single longitudinal yellow stripe on anterior surface; metasoma about 2× as long as wide; F1 2–3× as long as wide (Fig. 34); posterior ocellus separated from occipital carina by ⅓ to ½ its own diameter; oral fossa about 6–6.5× as broad as malar space (Fig. 3); body length 2.4–4.0 mm .... *occidentalis* Girault
– Foretibia without longitudinal yellow stripe; metasoma 1.1–1.4× as long as wide; F1 about 2× as long as wide (Fig. 37); posterior ocellus barely separated from occipital carina, often nearly touching it; oral fossa 4.0–5.0× as broad as malar space (Fig. 15); body length 1.8–2.1 mm .... *darleneae*, n. sp.
3. Female scape yellow to light brown; interscrobal area sculptured; mid-facial alveoli large, only 5–7 between eye margin and midline of face (Fig. 13); lateral surface of metasomal terga evenly alutaceous 4
– Female scape dark; interscrobal area smooth; mid-facial alveoli smaller, at least 8–9 between eye margin and midline of face (Figs. 10, 11); lateral surface of metasomal terga mostly smooth, with only a small alutaceous patch (Fig. 16) 5
4. Metasoma about 2× as long as wide, F1 3–4× as long as wide (Fig. 27) ....
.... *ashmeadi*, n. sp.
– Metasoma about 3× as long as wide, F1 5× as long as wide (Fig. 28) .... *teedoe*, n. sp.
5. Frontal grooves present, extending to margin of eye (Figs. 11, 12) 6
– Frontal grooves absent (Figs. 10, 15), if indicated medially, not extending to margin of eye 9
6. Scape 6× as long as wide (Fig. 33); speculum of forewing closed beneath submarginal vein (basal and cubital vein setae present) (Fig. 25) .... *ernobii*, n. sp.
– Scape 8–9× as long as wide (Figs. 29, 30); speculum of forewing open below submarginal vein (basal and cubital vein setae absent) (Figs. 23, 24) 7
7. Metasoma 2× as long as wide, posterior margin of second tergum excised medially (Fig. 22) .... *washingtoni* Girault
– Metasoma 2.5 or more × as long as wide, posterior margin of second tergum straight
.... 8
8. Foretibia with two longitudinal stripes, mid and hindfemora yellow except at base; F1 3.5× as long as wide (Fig. 30) .... *stephanopachi* Heqvist
– Foretibia without longitudinal stripes; mid and hindfemora dark except at apex; F1 5.5× as long as wide (Fig. 29) .... *methion* Walker

9. Midtibia almost entirely yellow, only with a small brown area at base; hindtibia at least half yellow ....*tachypterelli* Gahan
– Midtibia mostly dark, only a small yellow area at apex; hindtibia with apical ¼ or less yellow 10
10. Propodeum laterad of median carina alveolate or rugosely sculptured (Fig. 6) 11
– Propodeum laterad of median carina smooth or nearly so (Fig. 5) 12
11. Foretibia with 2 longitudinal stripes, F1 about 2× as long as wide, other funiculars longer than wide (Fig. 26); metasoma about 1.4× as long as wide; dorsal head width 3.0× length (Fig. 19) .... *anthonomi*, n. sp.
– Foretibia without longitudinal stripes; funiculars all about as long as wide (Fig. 40); metasoma about 1.1× as long as wide; dorsal head width 2.5× length (Fig. 17) ...
.... *leucopus* (Ashmead)
12. Metasoma 1.1–1.5× as long as wide 13
– Metasoma at least 2× as long as wide 14
13. OOL equal to OCL (Fig. 18); propodeum laterad of median carina smooth and shining (Fig. 5); foretibiae with stripes; F1 2.5–3× as long as wide (Fig. 38) ......*ergias* Walker
– OOL greater than OCL (as in Fig. 19); propodeum laterad of median carina with at least some light alutaceous sculpture; foretibiae without stripes; F1 1.5–2.0× as long as wide (Fig. 36) ....*columbianus* Ashmead
14. Metasoma 3.2–3.4× as long as wide ....*procerus*, n. sp.
– Metasoma less than 3× as long as wide, usually only about 2–2.5× 15
15. Foretibia with 2 longitudinal stripes; interocular distance 4× eye width (Fig. 20); malar space ½ eye height .... *pecki*, n. sp.
– Foretibia without longitudinal stripes; interocular distance 3× eye width or less (Fig. 21), malar space less than ½ eye height 16
16. F1 3× as long as wide (Fig. 39); area between toruli smooth (Fig. 10); length 2.5–3 mm .... *genei*, n. sp.
– F1 2× as long as wide or less (Figs. 35, 43); area between toruli alutaceous; length about 2 mm 17
17. F2 & 3 subquadrate (Fig. 35); dorsal head width 2.4× length (as in Fig. 17); forewing densely setose (Fig. 23), with setae under basal half of submarginal vein ....
.... *bigeloviae* Ashmead
– F2 & 3 longer than wide (Fig. 43); dorsal head width 3× length (as in Fig. 19); forewing sparsely setose and bare under basal half of submarginal vein (Fig. 24) ....
.... *robustus* (Crawford)

Entedon anthonomi, new species
Figs. 6, 19, 26, 48

Diagnosis. Foretibia with 2 longitudinal stripes; mid and hindtibia dark in basal half; eye height 2.5× malar space; metasoma about 1.5× as long as wide; frontal groove absent; interscrobes smooth; propodeum rugose or alveolate laterad of median carina (Fig. 6); F1 2× as long as wide, F2 & 3 1.5× as long as wide.

This species shares the evenly rugose propodeum with *leucopus*. It can be separated from that species by the foretibial stripes (absent in *leucopus*) and the longer funicular segments (all about as long as wide in *leucopus* (Fig. 40)). In other species which are similar (generally 1–3 mm and black bodied) the propodeum is nearly smooth or only lightly sculptured (e.g., *bigeloviae, robustus,* and *pecki*).

Description. Female length 2.0–2.2 mm. Color black, usually with some metallic
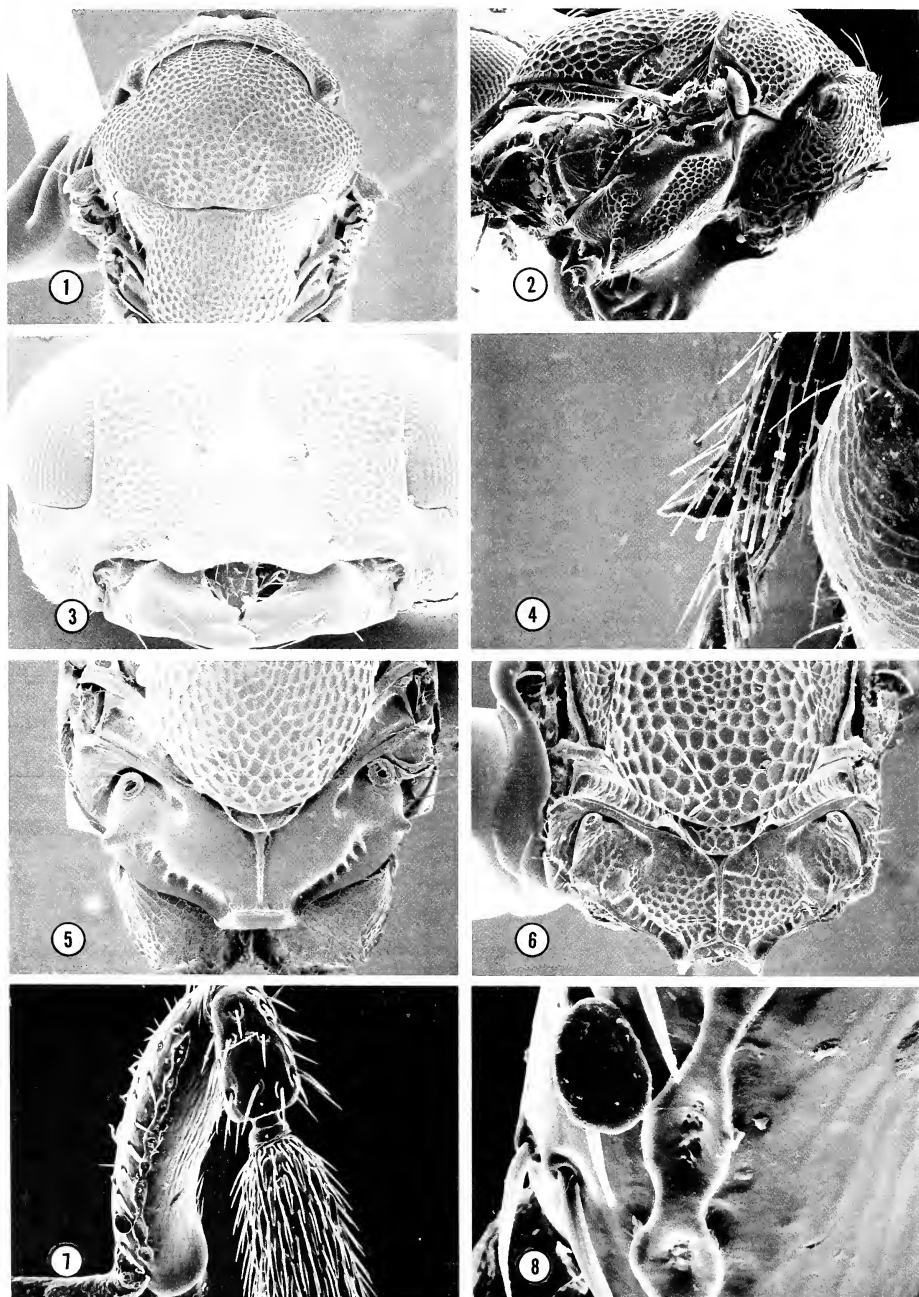
Figs. 1–8.   Scanning electron micrographs. 1. *E. darleneae,* dorsal thorax. 2–4. *E. occidentalis.* 2. lateral thorax. 3. mandibles. 4. foretibial spine. 5. *E. ergias,* propodeum. 6. *E. anthonomi,* propodeum. 7–8. *E. occidentalis* ♂. 7. scape. 8. anterior edge enlarged.

dark blue or blue green reflections on the dorsal thorax. Femora, and first two metasomal terga, mandibles, flagellum, basal half of mid and hindfemora, foretibia except at base and apex, femora except at apex, basal half of mid and hindtibia, metasoma, black to dark brown. Lateral surfaces of foretibia, fourth tarsomere of all legs brown. Tips of femora, anterior and posterior surface of foretibia, apical half of mid and hindtibia, tarsomeres 1–3 of all legs yellow.

Head: Mandibles not enlarged, teeth subequal in length. Clypeus truncate, oral fossa 1.5–1.8× malar space. Interscrobes smooth, space between toruli alutaceous. Toruli inserted above ventral margin of eye, mid facial alveoli of moderate size, about 8–9 between midline and margin of eye. Interocular distance 2.5–3.0× width of eye, eye height 2.5–3.0× malar space. Head width in dorsal view 3.0–3.8× length, frontal groove absent, POL:OOL:OCL 13:6:2. Antennae as in Figure 26.

Mesosoma: Mesoscutum with postero-medial alveoli small, surface dull in appearance. Scutellum slightly longer than wide, evenly alveolate or with few elongated alveoli antero-medially. Posterior margin of metanotum overlapping anterior propodeum. Propodeum (Fig. 6) rugose laterad of median carina, callus with 2 large setae and about 10 smaller ones.

Metasoma: Petiole (T1) wider than long, smooth. Metasoma 1.0–1.5× as long as wide, posterior margin of T2 straight, lateral surface smooth except for a small, alutaceous, setose area at antero-dorsal edge of each tergum.

Legs and wings: Foretibia with 2 longitudinal light stripes, without a curved spine at apex. Forewing hyaline, approximately 1.6× as long as broad, densely setose, marginal fringe present. Basal and cubital vein setae absent under submarginal vein, few subcubital setae present; ratio submarginal:marginal:stigmal:postmarginal 36:45:6:6. Marginal vein not swollen at base.

Male. Generally similar to the female except: head and thorax metallic green. First three tarsomeres of forelegs light brown to yellow. Antennae as in Fig. 48. Petiole conical and about as long as wide. Metasoma 1.6–1.8× as long as wide, without a basal yellow spot.

Hosts. Coleoptera, Curculionidae: *Anthonomus signatus* Say.

Distribution. Maryland, Ontario, New Brunswick.

Types. Holotype female on point with data: Maryland, Calvert Co., Chesapeake Beach, 13-VI-1985. L. Masner, sweeping (Deposited in USNM). Paratypes: 1♀ with same data as the holotype (USNM); 1♀, Virginia, Louisa Co., 4 mi S. Cuckoo, 18-V-1985, J. Kloke & D. R. Smith, Malaise trap (USNM); 27♀, 17♂, Ontario, Kempville, 26-VI-1974, Collector L. Masner; 1♀, Ontario, Oxford Mills, 21-V-1975, L. Masner; 1♀, Ontario, Blackburn, 9-VI-1939, O. Peck; 1♀, Ontario, Marmora, 1-5-VI-1952, J. R. Vockeroth; 1♀, Ontario, Leitrim [?, illegible], 14-VI-1940, O. Peck; 5♀, 3♂, New Brunswick, Washademoak, Sept., 1941, C. W. Maxwell; Ex. *Anthonomus signatus* (all CNC). 1♀, 1♂, New York, Lancaster, June 4, 1917 (UCR).

Etymology. The species epithet is derived from the generic name of the host, *Anthonomus.*

<p style="text-align:center">Entedon ashmeadi, new species
Fig. 27</p>

Diagnosis. Scape yellow; interscrobes alveolate, without smooth area; frontal grooves absent; facial alveoli large, only about 5 or 6 between scrobe and edge of eye (as in Fig. 13); F1 3–4× as long as wide (Fig. 27); metasoma 2× as long as wide, with terga
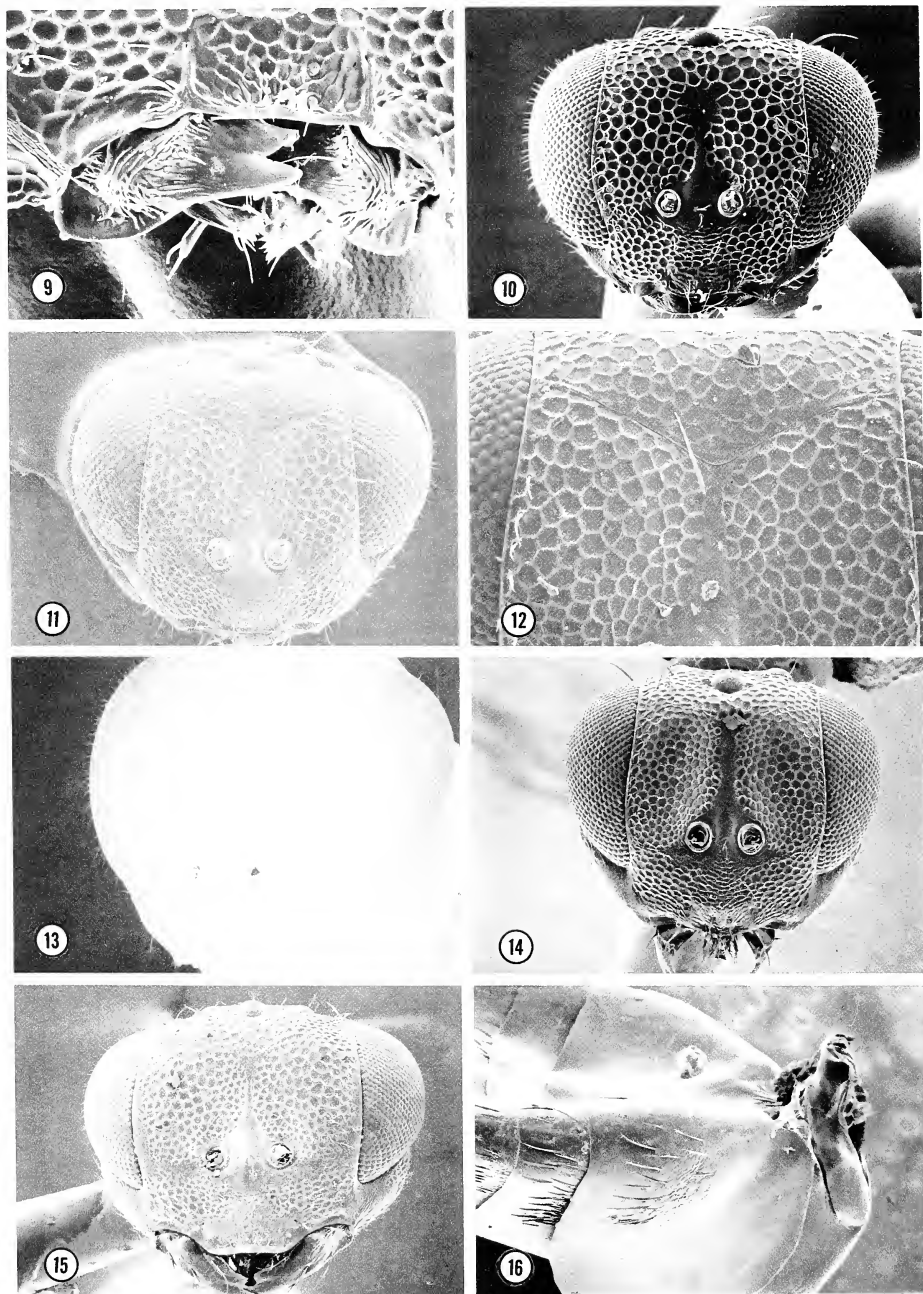
Figs. 9–16.   Scanning electron micrographs. 9–10. *E. genei.* 9. mandibles. 10. head. 11–12. *E. methion.* 11. head. 12. frontal groove. 13. *E. teedoe*, head (uncoated). 14. *E. ergias*, head. 15. *E. darleneae*, head. 16. *E. occidentalis*, lateral metasoma.

evenly sculptured laterally; foretibia with longitudinal stripes; mid and hindtibia yellow over at least half of length. Larger species, body length 3.7 mm.

This species is most closely related to *teedoe* with which it shares a yellow or light brown scape, the enlarged facial alveoli, and lack of a smooth interscrobal impression. It can be separated from that species by the length to width of the metasoma ($3\times$ as long as wide in *teedoe*) and F1 ($5\times$ as long as wide in *teedoe* (Fig. 28)).

Description. Female. Length 3.7–3.8 mm. Color as follows: head, mesosoma, second metasomal tergum, coxae, inner and outer lateral surface of foretibia irridescent blue-green. Antennal flagellum, mandibles, rest of metasoma, femora except posterodorsal tip dark brown. Scape yellow except light brown at apex. Foretarsi and 4th tarsomere of mid and hindleg light brown. Mid and hindtibia dark brown basally fading to light brown and then yellow at approximately the middle of the tibia. Postero-dorsal tip of mid and hindfemur, anterior and posterior surface of foretibia, and 1st three tarsomeres of mid and hindleg yellow.

Head: Mandibles with teeth subequal in length. Clypeus truncate, oral fossa $2.3\times$ malar space. Interscrobes alveolate, without smooth area, space between toruli sculptured. Toruli inserted above ventral margin of eye, mid facial alveoli large, only about 5–6 between midline and margin of eye. Interocular distance $2.3\times$ width of eye, eye height $3.8\times$ malar space. Head width in dorsal view $3\times$ length, frontal grooves absent, POL:OOL:OCL 25:6:5. Antenna as in Fig. 27.

Mesosoma: Mesoscutum with postero-medial alveoli larger, surface shiny in appearance. Scutellum longer than wide, medially with a line of elongate alveoli. Posterior margin of metanotum overlapping anterior propodeum. Propodeum with very weak alutaceous sculpture laterad of median carina, callus with 2 large and about 20 smaller setae.

Metasoma: Petiole (T1) wider than long, smooth. Metasoma $2\times$ as long as wide, posterior margin of T2 straight, lateral surface evenly alutaceous.

Legs and wings: Foretibia with 2 longitudinal light stripes, without a curved spine on anterior edge. Forewing hyaline, $2.5\times$ as long as wide, densely setose. Marginal fringe present. Basal and cubital vein setae absent under submarginal vein, ratio submarginal:marginal:stigmal:postmarginal 57:67:6:6. Marginal vein not swollen at base.

Male. Unknown.

Host. Unknown.

Distribution. Known only from Wisconsin.

Types. Holotype ♀ with data: "Wisconsin, Douglass Co. T43W, R11W, S11; Plot no. 14A, May 28, 1956. ex boxes containing Pj and overwintering Budworm, also *Petrova*" (Deposited in USNM). 3 paratype ♀♀ with same state and county, other data as follows: T44N 10W S16, Plot no. 16A, V-25-1956; T44N 10W S29, Plot no. 185, V-23-1956; T43W R11W S11, Plot no. 5Cre, V-28-1956. One paratype deposited in BMNH.

Etymology. This species is named in honor of W. H. Ashmead, one of the first hymenopterists at the U.S. National Museum.

<div align="center">

Entedon bigeloviae Ashmead
Figs. 23, 35

</div>

Entedon bigeloviae Ashmead, 1894:342.

Diagnosis. Foretibia without longitudinal stripes, metasoma 2× as long as wide; frontal groove absent; forewing densely setose, with setae under basal submarginal vein (Fig. 23); interscrobes smooth; area between toruli alutaceous; interocular distance 3× eye width, malar space ⅓ eye height; propodeum nearly smooth laterad of median carina; F1 1.5× as long as wide (Fig. 35), F2 and F3 quadrate; dorsal head width 2.4× length; body length 1.8–2.1 mm.

This species is most easily confused with *robustus, genei,* or *pecki* which are similar in size and black bodied. The presence of foretibial stripes and the longer malar space (½ eye height) distinguishes *pecki,* while *robustus* has the wings much more sparsely setose (Fig. 24), the dorsal head width is 3× the length, and F 2 and 3 are longer than wide (Fig. 43). F1 is 3× as long as wide in *genei* (Fig. 39) and the area between the toruli is smooth (Fig. 10).

Male.Unknown.

Hosts. Coleoptera, Curculionidae: *Epimechus* sp. on *Artemesia tridentata.*

Distribution. Western U.S. and Canada (also see notes below).

Types. Lectotype ♀ (present designation) on point with data: "N. Mex. [New Mexico], USNM type no. 2185. Two Paralectotype ♀♀ with same data (USNM).

Notes. Body length varies from 1.9–2.1 mm. There is color variation with some specimens markedly metallic green, while others are nearly entirely black. The legs may be black to brown and often with some purple cast. There is also some slight variation in the sculpturing of the dorsal thorax with the size of the alveoli on the scutum being larger in some specimens and giving more of a shiny appearance to the midlobe. The extent to which the alveoli on the scutellum are elongated also varies slightly, with some specimens nearly evenly alveolate.

There is a series of 4 specimens in the USNM collection from the Patuxent Wildlife Research Center, Prince George's Co., Maryland. Except for minor sculptural differences, I am unable to find any characters which might separate them from *bigeloviae.* However, since all the other specimens of this species are from the West I am reluctant to state definitely that these eastern specimens belong to the same species without additional material.

Other specimens examined. UNITED STATES. IDAHO. 1♀, Carey, Mar. 2♀♀, 1926, ex. bullet gall on *Artemesia tridentata* (USNM). MONTANA. 1♀, Wheatland Co., Deadman's Basin St. Rec. Area. 3,600'. 5-VI-1982 (CNC). NEVADA. 2♀♀, Arthur, I. LaRivers, 1937–38. *Artemesia tridentata* gall (USNM). TEXAS. 1♀, Del Rio, 10-V-1907. par. of *Epimechus.* Hunter no. 1423. 4♀♀, Devils River, 4-V-1907, bred from stem of *Sphaeralc. augustifol.* Hunter no. 1407. UTAH. 1♀, Logan, 10-IV-1933, bred from *Chrysothamnus* gall (USNM). CANADA. BRITISH COLUMBIA. 2♀♀, Walhachin. 23-IV-1954 (CNC).

Entedon columbianus Ashmead
Figs. 36, 49

Entedon columbiana Ashmead, 1888:103.
Entedon columbianus Ashmead. Peck, 1951.

Diagnosis. Mandibles with teeth subequal in length; clypeus truncate; frontal groove absent; foretibia without longitudinal stripes, mid and hindtibia dark except at apex;
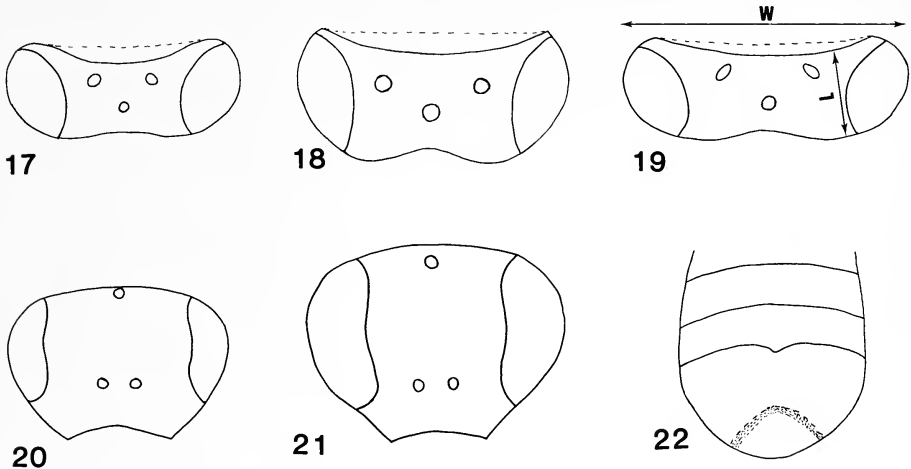
Figs. 17–22. 17–21. Female heads. 17. *E. leucopus,* dorsal. 18. *E. ergias,* dorsal. 19. *E. anthonomi,* dorsal. 20. *E. pecki,* frontal. 21. *E. robustus,* frontal. 22. *E. washingtoni,* dorsal anterior metasoma.

metasoma about 1.3–1.6× as long as wide; F1 about 1.5–2.0× as long as wide, F2, 3 about as long as wide (Fig. 36); OOL greater than OCL; propodeum lightly sculptured laterad of median carina then becoming smooth and shining. Body usually metallic green (or black) and about 2–3 mm in length.

This species is most easily confused with *E. ergias* which is about the same size, is usually metallic green, and otherwise similar in habitus. However, *ergias* has foretibial stripes, F1 is 2.5–3× as long as wide (Fig. 38), and OOL is equal to OCL (Fig. 18).

The males of *columbianus* have the metasoma 1.5–2.0× as long as wide, without an anterior yellow spot and F1 is 2–2.5× as long as wide and 1–1.5× as long as F2 (Fig. 49).

Hosts. Coleoptera, Curculionidae: *Apion occidentale* Fall (Black sunflower stem weevil). Hymenoptera: Tenthredinidae. *Euura exiguae* Smith, *E. lasiolepis* Smith, *E. geyerianae* Smith. *Pontania* sp. The parasitization of sawflys by species of *Entedon* has been questioned and most such records have been listed as doubtful (e.g., Boucek and Askew, 1968). The USNM and CNC collections contain series of specimens which are recorded from *Euura* species and these appear to be reliable. Considering that these sawfly hosts are gall formers in stems, the host habitat is not markedly different from that of other host taxa (e.g., *A. occidentale* in sunflower stems).

Distribution. Widespread throughout the United States and Canada.

Types. Holotype ♀ on point with data: "Washingtn [sic], D.C., USNM type no. 13146. *Entedon columbiana* Ashm." The specimen is missing the flagella of both antennae, all wings, right mid and hindleg, and left hindtibia and tarsi.

Notes. Body length varies from 1.7–2.6 mm. Smaller specimens tend to have the funicular segments shorter relative to their width. There are also some differences in
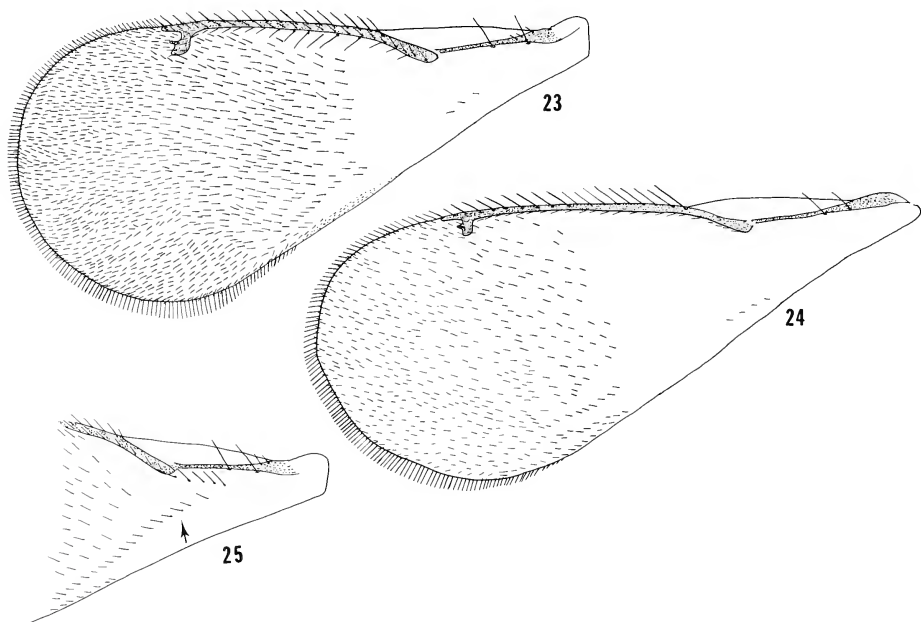
Figs. 23–25.   Forewings. 23. *E. bigeloviae.* 24. *E. robustus.* 25. *E. ernobii.*

the size of the individual alveoli on the face, frons, midlobe of the scutum, and median scutellum. There is some variation in coloration from distinctly blue green to green and some specimens have a small yellow patch on the apex of the foretibia which may extend about ¼ of the length (in some this appears to be an incomplete stripe). The metasoma varies from black to brown, although the first two terga are always metallic.

Other specimens examined. UNITED STATES. ARIZONA. 4♀♀, Baker no. 2123 (USNM). CALIFORNIA. 1♀, Fresno (USNM); 14♀♀, 9♂♂, Contra Costa Co., Antioch, 26-II-1967, ex. paratype series of *Euura (E.) exiguae, Salix exiguae* Nutt., *hiudsiana, melanopsis* (interior); 10♀♀, 5♂♂, Placer Co., 3.2 mi W. Emigrant Gap. 1,600 m, 23-IV-1968, Ex. paratypic series of *Euura (E.) lasiolepis,* Orange (interior) race; 1♀, Soda Springs, 6,760', 13-V-1966, ex. *Euura* stem gall on *Salix breweri* Bebb, or *S. lemmonii* Bebb (CNC). COLORADO. 9♀♀, Baker no. 1176; 1♀, Baker no. 2560; 1♀, Baker no. 1395; 1♀, Baker no. 1563; 15♀♀, 2♂♂, Colorado Springs, Hopkins no. 1202a, *Salix luteosericea,* various dates, May thru June; 1♀, Colorado Springs, Hopkins no. 10739, Salix; 3♀♀, N. Cheyenne Canyon, Hopkins no. 12082g & f July 29, 1915; 1♀, Douglas Co., Larkspur, Hopk. no. 12082f, on *Salix* with sawfly galls; 4♀♀, Larkspur, Hopkins no. 12081d & b; 1♀♀, Steamboat Springs, 9,000', 7-30-1953; 1♀, Ouray, 7-1-1937 (USNM), 1♀♀, Mt. Evans, Dolittle Ranch 9,800', 10-VIII-1961; 6♀♀, 2 mi. S. Meeker, 11-VII-1984; 1♀, Estes Park, 7,500' 20-VII-1961 (CNC). DISTRICT OF COLUM-BIA. 1♀, D.C., May 24, 1894 (USNM). ILLINOIS. 1♀, Mississippi Palisades, 11-VI-

1983; 1♀, Champaign Co., Univ. of Ill. South Farms, reared from *Salix* stem gall (USNM). INDIANA. 2♀♀, Lafayette, May, 1918 (USNM). IOWA. 5♀♀, 1♂, Sioux City, June 11, 1938; 1♀, reared from *Helianthus* stem; 1♀, May 28, 1928; 1♀, June, 1933; 1♀, May 13, 1919; 7♀♀, McGregor, March, 1919, reared from *Bidens* pith, Sioux City no. 1912 (USNM). KANSAS. 1♀, Lawrence, Nat. Hist. Res., 8-16-1956 (CNC). KENTUCKY. 1♀, Falmouth, 5-31-1917 (USNM). MAINE. 3♀♀, Bar Harbor. June 28, 1935, Par. Sawfly (USNM). MASSACHUSETTS. 1♀, Boston, IX-4-1909 (USNM). MICHIGAN. 1♀, Kent Co., 5-17-1959 (USNM). MINNESOTA. 1♀, Eaglesnest, July 9, 1959; 1♀, Olmstead Co. (USNM). MISSOURI. 7♀♀, 2♂♂, East St. Louis, *Helianthus annuus*; 3♀♀, 2♂♂, Maplewood, *Helianthus annuus,* from ? *Apion* (USNM); 1♀, Williamsville, 22-IV-13-V-1970 (CNC). NEBRASKA. 7♀♀, Thomas Co., Halsey, 1 mi W. July 1, 1983 (USNM). NEW JERSEY. 5♀♀, Arlington, IV-1928 (USNM). NEW MEXICO. 3♀♀, Albuquerque. Hopkins no. 10769e, *Salix*. May–June; 1♀, Mesilla; 1♀, Mesilla park, ex willow gall (USNM); 3♀♀, Lincoln Co., 2.4 Km. W. Alto, Hwy 532, 2200–2250, 25-VII-1982 (CNC). NEW YORK. 1♀, Utica, June (USNM). NEVADA. 6♀♀, 2♂♂, Reno, Hopkins no. 10784f, *Salix,* Feb.–Mar. (USNM). NORTH DAKOTA. 1♀, Minot; 9♀♀, 1♂, Cass Co., Vining's test plot n. of Casselton, 26 Oct. 1982, taken in cultivated *Helianthus annuus* L., emerged from *Apion occidentale* Fall (USNM). OHIO. 1♀, Wayne Co., Smartweed; 1♀, Columbus; 1♀, Summit Co., 6-9-1937 (USNM). OREGON. 1♀, Klamath Co., Beatty, 24-V-1967, Ex., paratypic series of *Euura* (*E.*) *geyerianae* (CNC). SOUTH DAKOTA. 1♀, Elk Point, Swept from Blue grass (USNM). UTAH. 1♀, Logan Can., 5,500', 4-29-1957 (USNM). VERMONT. 2♀♀, Rutland Co., 3 mi. E. Danby, 31 July 1979 (USNM). WYOMING. 1♀, Laramie, 40 mi. NE, 7-13-37 (USNM). CANADA. QUEBEC. 3♀♀, 13♂♂, Hull, 27-28-II-1957; 1♀, 2♂♂, Cap Rouge, 8-VII-1953; 1♀, Lac. Mondor, 13-VI-1951; 1♀, Harrington Lk., Gatineau Pk., 31-V-1954 (CNC). ONTARIO. 1♀, ex. *Pontania* sp., 1964 (USNM). 1♀, Bell's Corner, ex. *Pontania* sp., F.I. Survey, 13-II-1945; 1♀, Merivale, 7-V-1956, ex. gall on willow; 1♀, Ottawa, 22-V-1941; 1♀, Ottawa, 24-VI-1958; 2♀♀, 7-VII-1943; 1♀, 25-VII-1957; 1♀, 26-V-1960; 2♀♀, Rainy River, 3-VII-1960; 2;♀♀, Hwy. 15, Stittsville, 24-V-1970, Host *Hexomyia schineri*; 1♀, Constance Bay, 11-V-1941. 2♀♀, One Sided Lake, 13 July 1960 (CNC). MANITOBA. 1♀, Pipestone, 7-IV-1965; 3♀♀, Criddle Aweme, 28-III-1905 (CNC). SASKATCHEWAN. 1♀, Snowden, 26-VII-1944. ALBERTA. 2♀♀, Lethbridge, 5-VI-1956; 3♀♀, Waterton, 18-VI-1956, Swept from range grass; 4♀♀, 13.5 Mi. S. Drion, 14-VI-1982. 1♀, Elkwater Lake, 21-VII-1956. 8♀♀, Scandia, 26-VI-1956. Swept from range grass (CNC).

Entedon darleneae, new species
Figs. 1, 15, 37, 50

Diagnosis. Mandibles enlarged, bottom tooth longer than top tooth (Fig. 15); oral fossa 4–5.0× malar space; anterior margin of clypeus projecting forward over the mandibles; posterior ocellus separated from occipital carina by less than ½ its own diameter, often nearly touching the carina; F1 slightly less than 2× as long as wide (Fig. 37), F3 usually broader than long; metasoma about 1.0–1.4× as long as wide; foretibia without longitudinal stripes, anterior apex with curved projecting spine (as in Fig. 4); submarginal vein equal to marginal; 1.8–2.1 mm in length.
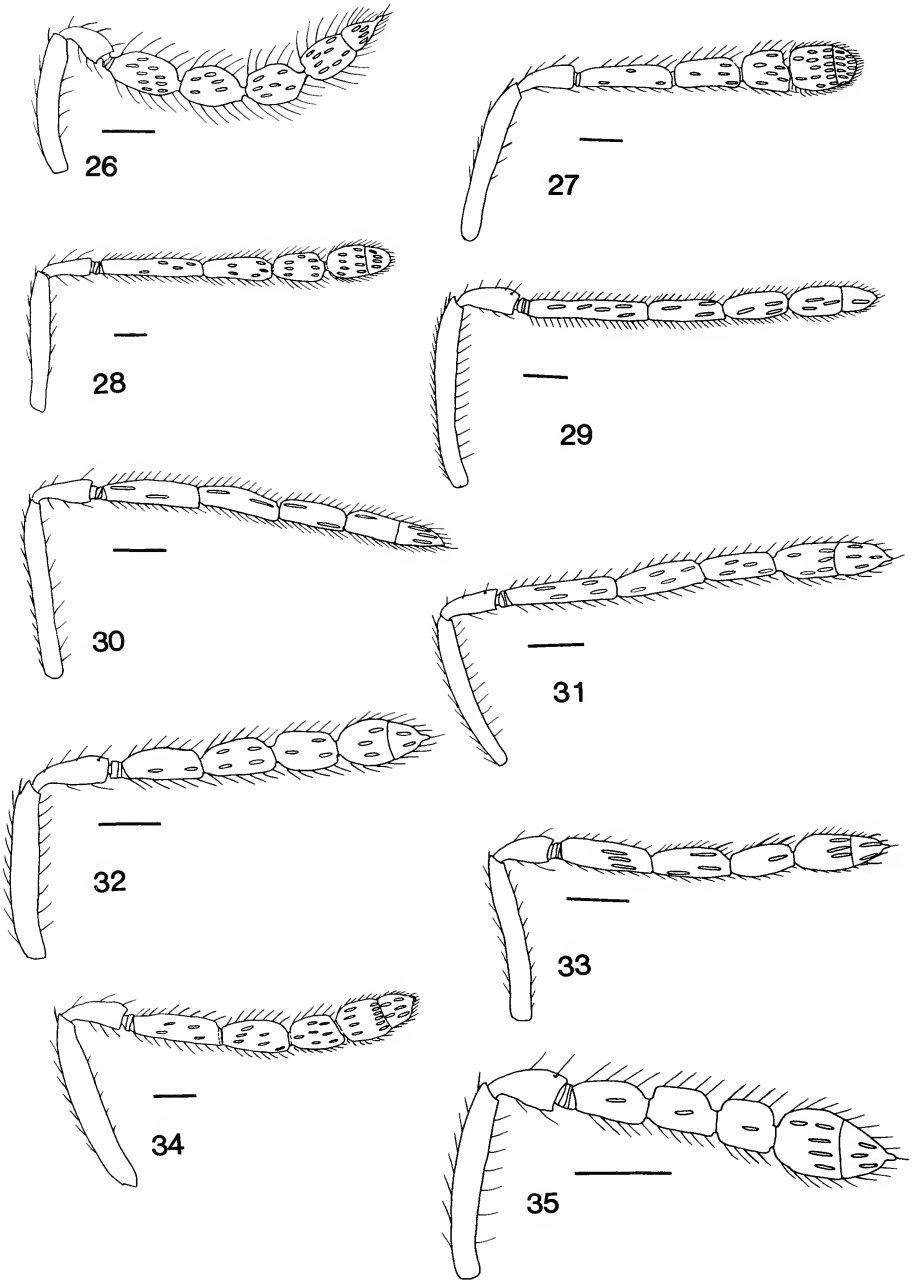
Figs. 26–35.   Female antennae. 26. *E. anthonomi.* 27. *E. ashmeadi.* 28. *E. teedoe.* 29. *E. methion.* 30. *E. stephanopachi.* 31. *E. washingtoni.* 32. *E. tachypterelli.* 33. *E. ernobii.* 34. *E. occidentalis.* 35. *E. bigeloviae.* Scale line equals 0.1 mm.

This species is most easily confused with *occidentalis* which shares the mandibles with larger lower tooth, projecting clypeus, and curved spine on the anterior surface of the foretibia. That species can be separated from *darleneae* by: oral fossa 6–6.5× malar space (Fig. 3), posterior ocellus separated from occipital carina by at least ½ its own diameter, foretibia with a single longitudinal stripe, F1 2–3× as long as wide (Fig. 34), metasoma 2× as long as wide, and body length 2.5–4.0 mm.

Description. Female. Length 1.8–2.1 mm. Color metallic green except the following: flagellum, mandibles, middle of tibia, foretarsi, last two mid and hind tarsomeres dark brown. Apex of femora and base of tibia, distal ⅕ to ⅛ of tibia, first 2 mid and hind tarsomeres yellow.

Head: Mandibles enlarged, with bottom tooth longer than top. Clypeus produced forward, oral fossa 4–5.0× malar space. Interscrobes smooth, space between toruli alutaceous. Toruli inserted above ventral margin of eye, mid facial alveoli moderate, about 10–12 between midline and margin of eye. Interocular distance 3.8× width of eye, eye height 3.2× malar space. Head width in dorsal view 3.3× length, frontal grooves absent, POL:OOL:OCL 18:7:1. Antennae as in Fig. 36.

Mesosoma: Mesoscutum with postero-medial alveoli larger, surface shiny in appearance. Scutellum longer than wide, medially with a line of elongate alveoli. Posterior margin of metanotum overlapping anterior propodeum. Propodeum smooth laterad of median carina, rarely with very weakly expressed alveoli, callus with 2 large setae and 10–15 smaller setae.

Metasoma: Petiole (T1) wider than long, smooth. Metasoma 1.0–1.4× as long as wide, posterior margin of T2 straight, lateral surface smooth except for a small, alutaceous, setose area at antero-dorsal edge of each tergum.

Legs and wings: Foretibia without longitudinal light stripes, with a curved spine at apex. Forewing hyaline, densely setose, approximately 2× as long as broad, marginal fringe present. Basal and cubital vein setae absent under submarginal vein, ratio submarginal:marginal:stigmal:postmarginal 25:25:4:4. Marginal vein not swollen at base.

Male. Similar to the female except the following: length 1.4–1.8 mm. Antennae as in Figure 50. Metasoma 1.8–2.0× as long as broad, without anterior yellow spot.

Hosts. Unknown.

Distribution. Midwestern and Western U.S. and Canada.

Types. Holotype ♀ on point with data: "Sioux City, Ia., Je., 11 [June], 1938. C. N. Ainslie collector (Deposited in USNM). Paratypes: COLORADO. 1♀, 2♂♂, 1582, Baker coll; 1♀, 1019, C. F. Baker collection (USNM); 1♀, Doolittle Ranch, 9,800′ Mt. Evans, 4-VIII-1961; 1♀, Echo Lake, 10,600′ Mt. Evans, July 26, 1961; 2♀♀, Loveland Pass West Slope, 9,850′, 28-VII-1961, (CNC). MICHIGAN. 1♀, Michigan Agr. College, #234; 1♀, Mich. (no other data) (USNM). MONTANA. 1♀, Gallatin Co., 23 Mi. NNW West Yellowstone, Beaver Ck., 6,500 ft., July 24, 1978, Sweeping flowering Alpine meadow (AMNH). NEW MEXICO. 1♀, 4♂♂, Las Cruces, 17 Apr., 1895, on *Sisymbrium* (USNM); 2♀♀, 1♂, Bluff Spring, Lincoln National Forest, 26-30 VII-1977, Malaise trap (CNC). WYOMING. 1♀, Battle L. Road, Sierra Madre Range, 18-VII-1961, 8,500′ (CNC). CANADA. ALBERTA. 5♀♀, 1♂, Scandia, 26-VI-1956; 1♀, Scandia, 11-VI-1956; 1♀, Lethbridge, 7-VII-1956; 1♂, Lethbridge, 25-VI-1956; 1♀, Lethbridge, 6-VII-1956; 3♀♀, Medicine Hat, 15-VII-1956; 4♀♀, McMurray, 30-
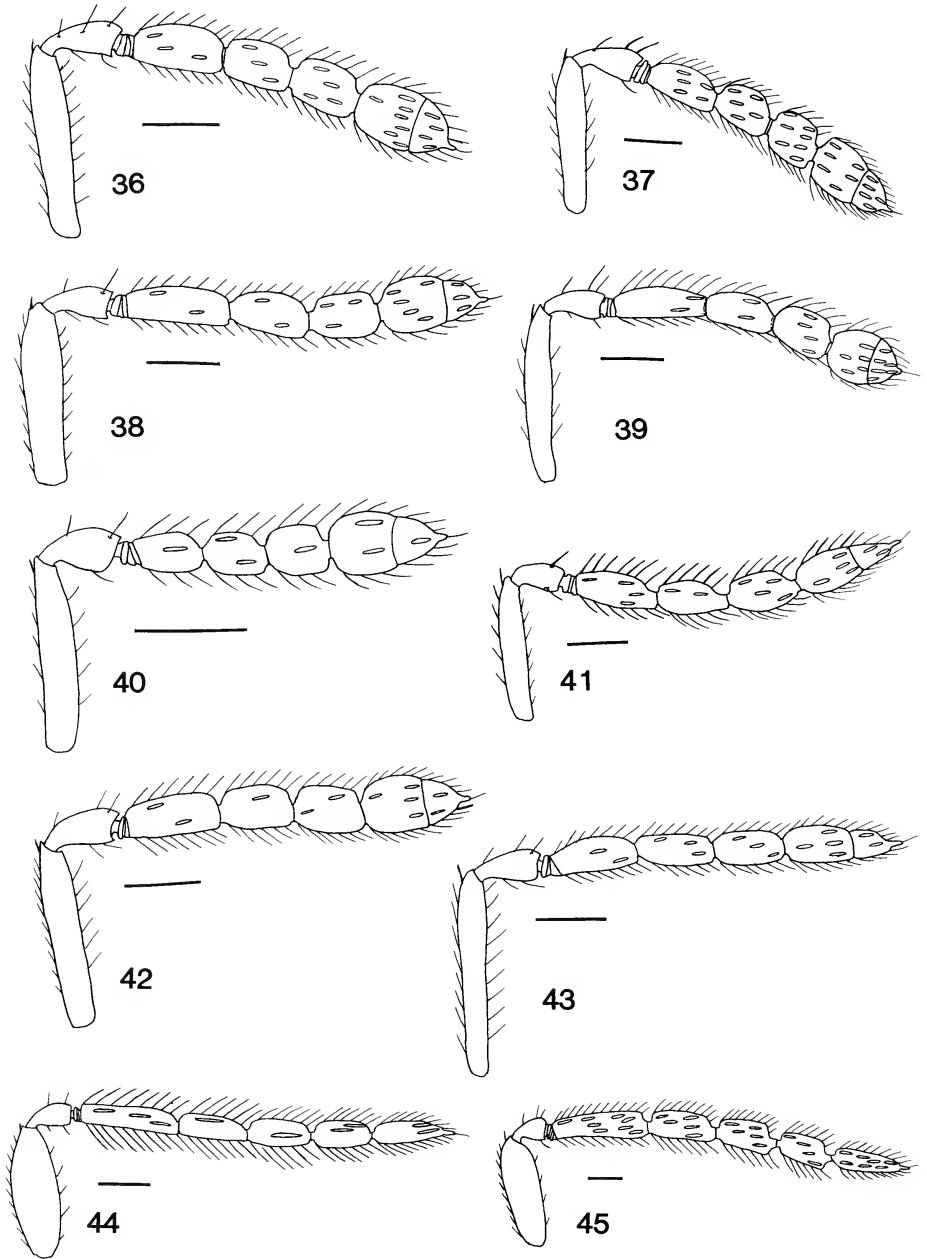
Figs. 36–45.   Antennae. 36–42. Females. 36. *E. columbianus.* 37. *E. darleneae.* 38. *E. ergias.* 39. *E. genei.* 40. *E. leucopus.* 41. *E. procerus.* 42. *E. pecki.* 43. *E. robustus.* 44–45. Males. 44. *E. teedoe.* 45. *E. stephanopachi.* Scale line equals 0.1 mm.

VII-1953; 1♀, McMurray, 8-VIII-1953; 1♀, Aspen Beach, Aug. 22, 1944, O. Peck (CNC). MANITOBA. 1♀, Brandon, 16-VII-1958 (CNC). NORTH WEST TERRITORIES. 1♂, Yellowknife, 19-VIII-1949; 1♀, Norman Wells, 10-VII-1949 (CNC). ONTARIO. 1♀, Ottawa, 10-17 VII-1979 (CNC). SASKATCHEWAN. 1♀, Snowden, 28-VII-1944; 2♀♀, 1♂, White Fox, 10-VII-1944; 1♀, White Fox, 11-VII-1944 (CNC).

Etymology. This species is named in honor of my mother Darlene M. Schauff.

Entedon ergias Walker
Figs. 5, 14, 18, 38, 55

Entedon ergias Walker, 1839:100.
Entedon busiris Walker, 1839:99.
Entedon merion Walker, 1839:100.
Elachestus annulatus Förster, 1841:39.
Ichneumon leucogramma Ratzeburg, 1844:170.
Eulophus albipes Ratzeburg, 1844:165.

Diagnosis. Frontal groove absent; interscrobes smooth; OOL equal to OCL (Fig. 18); F1 2.5–3× as long as wide (Fig. 38); foretibia with 2 longitudinal light stripes (see below) (males with 2 distinct stripes); propodeum laterad of median carina smooth; metasoma only about 1.2× as long as wide. Body color generally black or dark metallic green and about 1.8–2.5 mm in length.

Males of *ergias* have the metasoma about 1.3–2× as long as wide and with a large basal yellow spot. The midtibia may be almost entirely yellow or with the basal ¼–⅓ light brown. F1 is about 3× as long as wide and 1.5× as long as F2 (Fig. 55).

This species is most easily confused with *E. columbianus,* which is similar in habitus. However, *columbianus* can be differentiated by the lack of foretibial stripes, F1 1.5–2.0× as long as wide (Fig. 36), and OOL greater than OCL.

Hosts. Coleoptera, Scolytidae: *Scolytus multistriatus* (Marsham) (smaller European elm bark beetle), *S. rugulosus* (Muller) (shot hole borer). Several other hosts are recorded for Europe (Boucek and Askew, 1968), including *Scolytus scolytus* Fabricius, *S. mali* (Bechstein) (larger shothole borer), *S. intricatus* (Ratzeburg), and *s. ratzeburgi* Janson. As noted by Beaver (1966), there are also records of this species attacking *Pityogenes bidentatus* (Herbst) (Scolytidae) and *Magdalis armigera* (Geoffroy) (Curculionidae) which are considered as questionable.

Distribution. Eastern U.S. and Canada. Europe.

Types. The type of this species is in the British Museum (Graham, 1963) and I have not examined it. This species, however, is readily recognizable and I have studied reliably identified specimens from Europe.

Notes. Length varies from 1.8–2.3 mm (up to 2.8 mm in some European specimens). Some larger European specimens also may have the metasoma as much as 1.6× as long as wide. General body color ranges from black to metallic green or blue green. Although most specimens have the propodeum laterad of the median carina completely smooth, they may occasionally have some very light indication of alutaceous sculpture. Graham (1971) and others have noted that this species has the sculpturing on the dorsum of the thorax very weakly raised from the surface. While this is true,
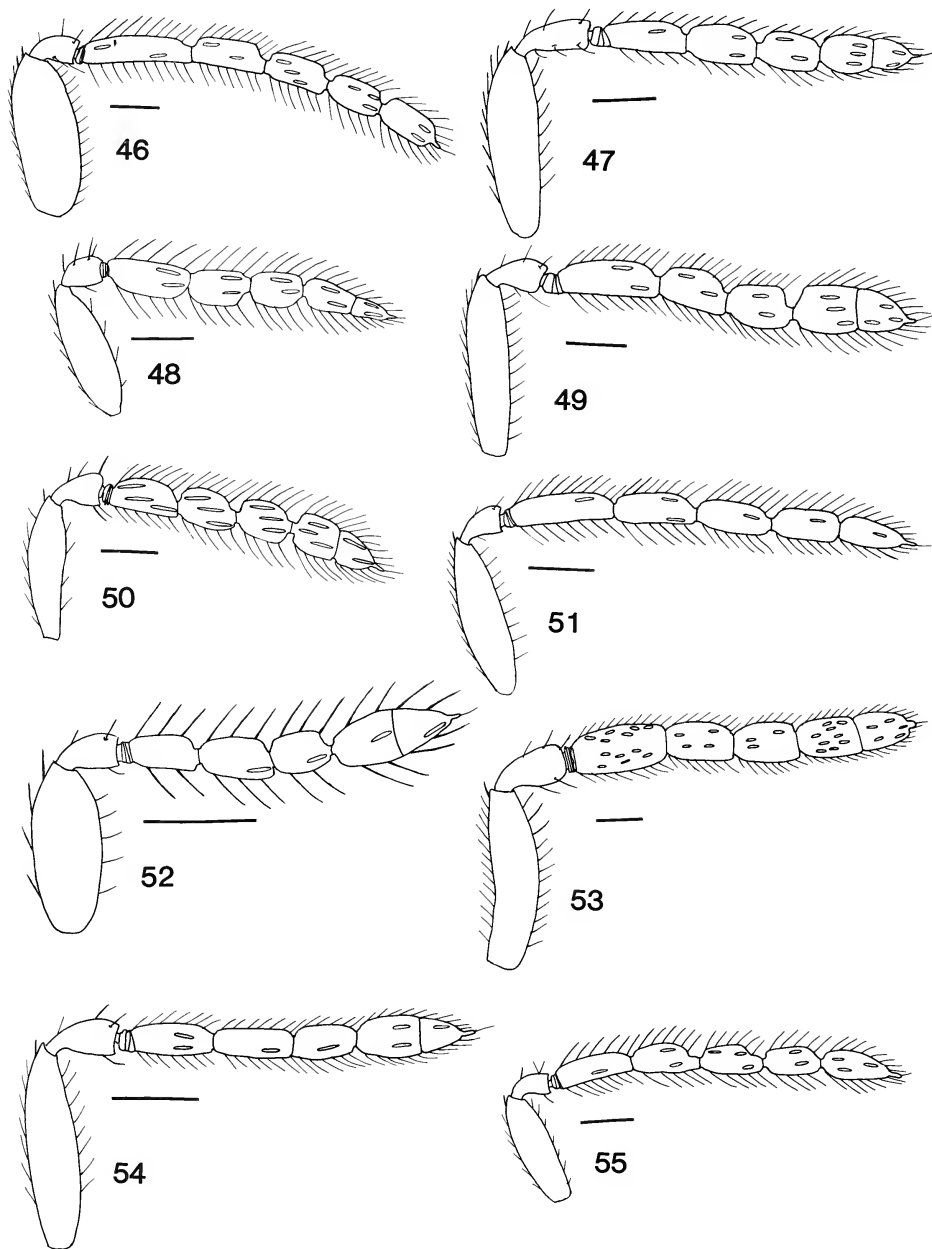
Figs. 46–55.   Male Antennae. 46. *E. methion.* 47. *E. tachypterelli.* 48. *E. anthonomi.* 49. *E. columbianus.* 50. *E. darleneae.* 51. *E. ernobii.* 52. *E. leucopus.* 53. *E. occidentalis.* 54. *E. robustus.* 55. *E. ergias.* Scale line equals 0.1 mm.

it is difficult to assess this character without other specimens for comparison. Some specimens have the longitudinal stripes on the foretibia present only as slightly lighter areas than the rest of the tibia or with the stripes fading toward the middle of the tibia.

For many years this species was cited in the literature as *E. leucogramma* (Ratzeburg). That name was recognized as a junior synonym of *E. ergias* by Boucek and Askew (1968). This species has been introduced into the United States from Europe for the control of elm bark beetles. The life history and immature stages of this species was studied by Beaver (1966). Its biology is unusual in that the female enters the gallery of the scolytid host and oviposits in the egg. However, the parasite does not complete its development until the host larva is quite large. This egg-larval mode of development is uncommon in chalcidoids and especially in Entedoninae.

Specimens examined. UNITED STATES. CALIFORNIA. 1♀, Heraldsburg, 7-21-1944, at entrance of shot-hole borer (USNM). CONNECTICUT. 1♀, 1♂, New Haven, Sept. 12, 1957, reared elm; 1♀, Fairfield, Mar. 1, 1934, Hopk. no. 17620c, ex. *S. multistriatus* (USNM). IOWA. 1♂, Hamburg, V-28-1953, ex. *S. rugulosus* (USNM). NEW YORK. 2♂♂, Rockland Co., 1 June, 1936, Bred from Elm; 1♀, 3♂♂, Yonkers, 3 Aug., 1937, C.U. invest. Dutch Elm Dis.; 1♀, 1♂, Pearl River, June 5, 1936, C.U. Inves. Dutch Elm Dis.; 1♀, 3♂♂, Westchester Co., Lowr., Reared elm (USNM). NORTH CAROLINA. 2♀♀, 1♂, Durham, Oct. 6, 1941, Reared, Host: *S. rugulosus* (USNM). OHIO. 1♀, Barberton, 6-30-1936; 2♀♀, Warren, Aug. 26, 1939 ex. *S. rugulosus* (USNM). PENNSYLVANIA. 2♀♀, Allegheny Co., ex. elm branches infested with *S. multistriatus*; 1♀, 1♂, Chestnut Hill, XII-27-1958, reared *S. rugulosus*; 6♀♀, Hatboro, June 8, 1922, from trees infested with scolytidae; 6♀♀, 4♂♂, Dauphine Co., Middleton, 18-VIII-18-X, 1977, ex. American elm (USNM). SOUTH CAROLINA. 1♂, Clemson (USNM). VIRGINIA. 1♀, Fairfax Co., nr. Annandale, V-30-31, 1981, Malaise trap; 1♀, Alexandria, Dec. 1, 1970, *Scolytus rugulosus* (USNM). CANADA. ONTARIO. 2♀♀, 1♂, Toronto, 20-VII-1970, ex. elm log with scolytid beetles; 2♀♀, 3♂♂, Toronto, 22-VI-1971, ex. *Scolytus multistriatus*; 1♀, Brampton, 20-IX-1966, Host: *Scolytus multistriatus*; 2♀♀, 2♂♂, Belfountain, F.I.S., 70-595 ex. *S. multistriatus*; 1♀, Rondeau Park, 22-VI-1922. QUEBEC. 1♀, 1♂, St. Hilaire, 4-IX-1968, ex. *Scolytus rugulosus* (CNC). NOVA SCOTIA. 2♀♀, Crosby, Sept. 23, 1952, taken on apple (CNC). Also about 28 specimens from Europe (CNC, USNM).

Entedon ernobii, new species
Figs. 25, 33, 51

Diagnosis. Foretibia without stripes; frontal grooves present; metasoma 2× as long as wide, posterior margin of T2 straight; forewing (Fig. 25) with cubital and basal vein setae present (speculum closed); antennae (Fig. 33) with scape 6× as long as wide, F1 4× as long as wide; midtibia with basal ½ brown, remainder yellow.

This species is most easily confused with *methion, stephanopachi,* and *washingtoni* which also have the frontal grooves present. All of these other species have the speculum open (as in Figs. 23, 24) (basal and cubital vein setae absent under submarginal). In addition, *washingtoni* has the second metasoma tergum excised medially (Fig. 22), *stephanopachi* has foretibial stripes, and *methion* has F1 5.5× as long as wide (Fig. 29).

Description. Female. Length 2.1–2.5 mm. Color black, usually with some metallic dark blue or blue green reflections on the first two metasomal terga. Mandibles,

antennae, metasoma except basal segments dark brown to black. Apex and base of all femora and tibia, apical $\frac{1}{4}$ to $\frac{1}{5}$ of tibia, first 3 tarsomeres of all legs yellow.

Head: Mandibles not enlarged, teeth subequal in length. Clypeus truncate, oral fossa 1.5–1.7× malar space. Interscrobes smooth, space between toruli alutaceous. Toruli inserted above ventral margin of eye, mid facial alveoli moderate, about 8–9 between midline and margin of eye. Interocular distance 2.5–3.0× width of eye, eye height 2.0–2.2× malar space. Head width in dorsal view 2.7–3.0× length, frontal groove present, POL : OOL : OCL 13:6:3. Antenna as in Figure 33.

Mesosoma: Mesoscutum with postero-medial alveoli moderate in size, surface shiny in appearance. Scutellum longer than wide, evenly alveolate or with few elongated alveoli antero-medially. Posterior margin of metanotum overlapping anterior propodeum. Propodeum smooth to lightly alveolate laterad of median carina, callus with 2 setae and about 6 smaller ones.

Metasoma: Petiole wider than long, smooth. Metasoma 1.5× as long as wide, posterior margin of T2 straight, lateral surface smooth except for a small, alutaceous, setose area at antero-dorsal edge of each tergum.

Legs and wings: Foretibia without longitudinal light stripes, without a curved spine at apex. Forewing hyaline, approximately 2.4× as long as broad, densely setose, marginal fringe present. Basal and cubital vein setae present under submarginal vein (speculum closed) (Fig. 25), few subcubital setae present, ratio submarginal : marginal : stigmal : postmarginal 37:46:5:5. Marginal vein not swollen at base.

Male. Generally similar to the female except: body length 1.9–2.2 mm; head and thorax usually more distinctly metallic green. Antenna as in Figure 51. Interocular distance 3.4× eye width. Petiole conical and about as long as wide. Metasoma 2.5× as long as wide, without a basal yellow spot.

Hosts. Coleoptera, Anobiidae: *Ernobius pinicola* Ruckes, *E. melanoventris* Ruckes.

Distribution. California and Nevada.

Notes. The darkened areas of the mid and hindtibia vary from black to brown. The tarsomeres of the foreleg, and the apical tarsomeres of the mid and hindleg vary from yellow to light brown.

Types. Holotype female on point with data: "California, Tuolumne Co., Pinecrest. VI-5-1957. ex. cones of *Pinus jeffreyi.* H. Ruckes, Jr. No. 290" (Deposited in USNM). Paratypes as follows: CALIFORNIA. 10♀♀, 6♂♂, Cuyamaca St. Pk., Green View Meadow, ex. *Ernobius pinicola* & *E. melanoventris* on *P. jeffreyi* and *P. monophylla,* various dates from Jan. 1956-Aug. 1957, H. Ruckes, Jr.; 1♀, 1♂, San Diego Co., Cuyamaca, ex. *Ernobius* sp. cones of *Pinus jeffreyi,* H. Ruckes; 1♀, 2♂♂, Siskyou Co., Lava Beds Natl. Pk., 22-VII-1953. NEVADA. 3♀♀, 1♂, Storey Co., Crystal Bay, 3-X-1955. ex cones of *Pinus ponderosa,* H. Ruckes, Jr. All paratypes in USNM except one pair in CNC and BMNH.

Etymology. This species is named for the genus of the known hosts, *Ernobius.*

Entedon genei, new species

Figs. 9, 10, 39

Diagnosis. Foretibia without longitudinal stripes; interscrobes smooth and area between toruli smooth (Fig. 10); frontal groove absent; F1 3× as long as wide (Fig.

39); propodeum laterad of median carina smooth or very lightly alutaceous; metasoma $2\times$ as long as wide. Larger species, body length 2.5–3.1 mm.

This species is most easily confused with *robustus* or *bigeloviae* which are also black bodied, lack foretibial stripes, are without frontal grooves, and have the median propodeum lightly sculptured. It can be separated by the length of F1 (1.5 or $2.0\times$ as long as wide in the other species (Figs. 35, 43)) and the area between the toruli is smooth (alutaceous in other species). Additionally, *robustus* has the forewing with much sparser setation (Fig. 24).

Description. Female. Length 2.5–3.1 mm. Color black, usually with some metallic dark blue or purplish reflections on the dorsal thorax. Femora, and first two metasomal terga, mandibles and fourth tarsomere of all legs brown. Apices of femora, apical $\frac{1}{4}$–$\frac{1}{5}$ of tibia, first 3 tarsomeres of all legs yellow.

Head: Mandibles not enlarged, teeth subequal in length; clypeus truncate, oral fossa 2.0–$2.5\times$ malar space. Interscrobes smooth, space between toruli smooth. Toruli inserted above ventral margin of eye, mid facial alveoli moderate, about 8–9 between midline and margin of eye. Interocular distance $2.6\times$ width of eye, eye height $3.0\times$ malar space. Head width in dorsal view $2.8\times$ length; frontal grooves absent, POL : OOL : OCL 18:7:2. Antennae as in Figure 39.

Mesosoma: Mesoscutum with postero-medial alveoli large, surface shiny in appearance. Scutellum longer than wide, evenly alveolate. Posterior margin of metanotum overlapping anterior propodeum. Propodeum smooth or very lightly alutaceous laterad of median carina, callus with 2 large and about 15 to 20 smaller setae.

Metasoma: Petiole (T1) wider than long, smooth. Metasoma $2.0\times$ as long as wide, posterior margin of T2 straight, lateral surface smooth except for a small, alutaceous, setose area at antero-dorsal edge of each tergum.

Legs and wings: Foretibia without longitudinal light stripes, without a curved spine at apex. Forewing hyaline, $2.0\times$ as long as wide, densely setose, marginal fringe present. Basal and cubital vein setae absent under submarginal vein, few subcubital setae present; ratio submarginal : marginal : stigmal : postmarginal 28:30:3:3. Marginal vein not swollen at base.

Male. Unknown.

Hosts. Unknown.

Distribution. Northeastern U.S. and Canada.

Types. Holotype female on point with data: "USA, New York, Long Island, South Haven, June 1–9, 1974. M Kamran" (Deposited in AMNH). Paratypes: 2♀♀, same locality as holotype with collection dates of VI-19-1974 (AMNH) and June 23–30, 1976 (USNM). 1♀, RHODE ISLAND, Westerly, VI-20-1936, M. Chapman (AEI). 2♀♀, NEW YORK, Ithaca, Coll. F. H. Chittenden (USNM). 1♀, Flatbush, 25-V-1894, J. L. Zabriskie, 615 *Entedon,* parasite on 614 (USNM). 1♀, Otsego, VII-3-1935, H. K. Townes (AEI). 3♀♀, New Brunswick, Kouchibouguac N.P., 11-12-VII-1977. M. Ivanochko. code 5594D (CNC). 1♀, on plastic card with red label "*Metacolus conicus*" [other writing illegible] (CNC). 1♀, with red tag that reads "Bathroom, III, Cooper" (CNC).

Etymology. This species is named in honor of my father Leo E. Schauff, known to his friends as Gene.

Entedon leucopus (Ashmead)
Figs. 17, 40, 52

Pleurotropis leucopus Ashmead, 1888:102.
Entedon leucopus (Ashmead). Peck, 1951.

Diagnosis. Foretibia without longitudinal stripes, metasoma 1–1.2× as long as wide; frontal grooves absent; interscrobes smooth; propodeum rugose or alveolate laterad of median carina then becoming smooth towards spiracle; F1 1.5× as long as wide (Fig. 40), F2 and F3 quadrate; dorsal head width 2.5× length (Fig. 17). Body length 1.1–1.5 mm, color black.

Males have the head metallic blue green. The antenna (Fig. 52) has F4 and F5 forming a club. The metasoma is 1.9× as long as wide, and with a light brown spot antero-dorsally. The mid and hindtibia are yellow in apical half.

This species shares the rugose propodeum with *anthonomi* and can be separated from it by the absence of foretibial stripes (present in *anthonomi*) and the shorter funicular segments (all segments longer than wide in *anthonomi* (Fig. 26)). In addition, the alveolate sculpture of the vertex and the mid lobe of the scutum is weak in *leucopus,* the individual alveoli large (about equal in diameter to an ocellus) and the surface appears shiny. The sculpture of *anthonomi* is much coarser, the individual alveoli smaller, and the appearance of the head and scutum is dull by comparison. The size of individual alveoli seems to vary with size and may also vary with host. I am therefore reluctant to place too much emphasis on this character.

Hosts. Unknown.

Distribution. Only known from Florida, Ontario, and Quebec.

Types. Lectotype ♀ (present designation) on pin with 4 card mounts containing 5 specimens. The lectotype is on the third card from the top and has been marked with a black arrow on the card. The only data attached to the specimens is a small card with the name "*Pleurotropis leucopus* Ashm." and a small red USNM type card with the number "41375" (Ashmead indicated Florida as the type locality in the original publication). There are 12 paralectotype females on three other pins. Lectotype and paralectotype labels have been attached to each pin (all USNM).

Notes. Some variation was observed in the amount of yellow on the mid and hindtibia. Most specimens have only the distal ¼ yellow, but two females had the yellow coloration extended for ⅓ to ½ the length of the tibia.

Other specimens examined. CANADA. ONTARIO. 1♀, Ottawa, 3-VI-1940; 1♀ Bell's Corner, 23-V-1945 (CNC). QUEBEC. 1♀, Cap Rouge, 8-VII-1953; 1♀, Laniel, 14-VI-1941; 1♀, Gatineau Pk., 13-VI-1980 (CNC).

Entedon methion Walker
Figs. 11, 12, 29, 46

Entedon methion Walker, 1839:105.
Entedon gyorfii Erdös, 1954:348.

Diagnosis. Frontal grooves present (Fig. 12); scape 8–9× as long as wide, F1 5.5× as long as wide (Fig. 29); malar space nearly half of eye height; foretibia without longitudinal stripes; metasoma 3–4× as long as wide; mid and hind femora dark

brown except at apex. Body color is generally black. This is a generally larger species with body length ranging from 3.0–3.5 mm (about 2.5 mm for males).

Males have some metallic green or blue on the head and thorax. The metasoma is about 2× as long as wide and without an anterior yellow spot. F1 is 5× as long as wide with F2 3× as long as wide and F5 clearly separated from the other funiculars (Fig. 46).

This species is most easily confused with *stephanopachi, washingtoni,* and *ernobii* which also have the frontal grooves present. It can be separated from them by: foretibial stripes present and mid and hindtibia yellow except at base in *stephanopachi*; metasoma 2× as long as wide in *washingtoni;* speculum closed in *ernobii* (Fig. 25).

Hosts. Coleoptera, Anobiidae: *Ernobius mollis* L. In Europe, *methion* is also recorded from *Ernobius nigrinus* Sturm and *Ips acuminatus* Gyllenhal (Scolytidae).

Types. I have not examined the type of this species which is in the British Museum (Graham, 1971). However, this species is quite distinctive and I have studied specimens determined by Z. Boucek who has examined the type.

Distribution. Eastern U.S., Colorado, and Europe.

Notes. Foretarsi may be yellow to dark brown; sculpture of propodeum from lightly alutaceous to lightly rugose.

Other specimens examined. UNITED STATES. MAINE. 1♀, Mt. Desert, July 31, 1922 (USNM). RHODE ISLAND. 1♀, Tiverton, Mar. 23, 1951 (USNM). MARYLAND. 1♀, Plummers Island, 6-VI-1913, *Acer,* Hopkins no. 11338 (USNM). MASSACHUSETTS. 2♀♀, 2♂♂, Worcester, July 27, 1917, Par. *Ernobius mollis, Pinus* (USNM). COLORADO. 1♀, 1♂, El Paso Co., reared July 8, 1915, *Pinus flexilis* Hopkins no. 12421 (USNM). I have also examined several European specimens determined by Z. Boucek (USNM).

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Entedon occidentalis Girault
Figs. 2, 3, 4, 7, 8, 16, 34, 53

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Entedon occidentalis Girault, 1916b:48

Diagnosis. Mandibles enlarged, oral fossa 6–6.5× malar space, bottom tooth longer than top tooth (Fig. 3), anterior margin of clypeus projecting forward. Posterior ocellus separated from occipital carina by about ½ to ⅔ its own diameter. F1 2.0–3× as long as wide (Fig. 34), F2 & 3 at least as long as wide. Metasoma about 2× as long as wide. Foretibia with a single light longitudinal stripe, anterior apex with curved projecting spine (Fig. 4). Submarginal vein equal in length to marginal. Generally larger species, 2.5–4.0 mm in length, with color predominately metallic green.

The males of *occidentalis* have the metasoma about 1.3× as long as wide and without a basal yellow spot. The antenna is as in Fig. 53.

This species is most easily confused with *darleneae* which shares the enlarged mandibles with bottom tooth longest and the projecting clypeus. In *darleneae,* the following characters differ from above: oral fossa 4–5.0× malar space, F1 less than 2× as long as wide and F3 at least as long as wide (Fig. 37), metasoma 1–1.4× as long as broad, foretibia without a longitudinal stripe.

Hosts. Unknown.

Distribution. Western U.S. and Canada.

Types. Girault apparently described this species from 7 specimens, but only designated two females from Los Angeles as types. Both of these specimens bear USNM type labels (no. 19626). The lectotype (present designation) is missing one forewing and three of the four tarsomeres of the left fore and hindleg. One fore and hindwing have been slide mounted. The paralectotype has been knocked from the point and badly damaged. It has been remounted, but the wings, 1 antenna, and most of the legs are missing (one antenna and one hindleg were slide mounted by Girault).

Other specimens examined. UNITED STATES. CALIFORNIA. 1♂, Fieldbrook, 28-V-1903; 1♀, Monterrey Co., Arroyo Seco Camp, 3 May, 1964 (USNM); 1♀, Apple Valley, 9-V-1955 (CNC). COLORADO. 1♀, Boulder, 5,500' June 9, 1961; 1♂, Jefferson, 9,400', 14-VII-1961 (CNC). KANSAS. 2♀♀, (no other data) (USNM). UTAH. 1♀, Wasatch, 27-6. 2♀, Logan Canyon, 5,500', V-29-1957 (USNM). MONTANA. 15♀♀, 19♂♂, Wheatland Co., Deadmans Basin St. Rec. Area. 3,600', 5-VI-1982 (CNC). NEVADA. 1♀, Mercury, 11 June, 1965 (USNM). CANADA. ALBERTA. 1♀, Lethbridge, 18-VI-1950; 1♀, Lethbridge, May 18, 1934; 1♀, Berwyn, July 15, 1940 (CNC). BRITISH COLUMBIA. 6♀♀, 1♂, Oliver, White Lake, 28-V-1959; 1♀, Oliver, Vaseaux L., 29-V-1959; 1♀, Kamloops, Paul L. 29-VI-1950 (CNC).

Entedon pecki, new species
Figs. 20, 42

Diagnosis. Foretibia with 2 longitudinal stripes; interocular distance 4× eye width (Fig. 20), malar space ½ eye height; propodeum with some lightly rugose sculpture immediately laterad of median carina, then becoming smooth. Metasoma 2.2–2.5× as long as broad.

This species is very similar to both *robustus* and *bigeloviae* which are about the same size, have the metasoma about 2× as long as wide and are generally black bodied. It can be separated from those species by the longer malar space relative to the height of the eye (¼ eye height in *robustus* and ⅓ eye height in *bigeloviae*) and the broader interocular space (slightly less than 3× in *bigeloviae* and *robustus* (Fig. 21)). In addition, neither of those species have foretibial stripes and the area between the toruli is sculptured. *E. anthonomi* has foretibial stripes, but the metasoma of that species is shorter (about 1.5× as long as wide) and the propodeum is almost uniformly rugose (Fig. 6).

Description. Female. Length 2.0–2.2 mm. Color black, with some bronze or dark blue green reflections on the first two metasomal terga. Mandibles, lateral surface of foretibia brown. All tarsomeres of foreleg and fourth tarsomere of mid and hindlegs brown. Apices of femora, apical ¼ to ⅕ of mid and hindtibia light yellow to white.

Head: Mandibles not enlarged, teeth subequal in length. Clypeus truncate, oral fossa 1.4–1.5× malar space. Interscrobes smooth, area between toruli alutaceous. Toruli inserted at ventral margin of eye, mid facial alveoli moderate, about 8–9 between midline and margin of eye. Interocular distance 4.0× width of eye, eye height 1.8–2.0× malar space. Head width in dorsal view 3.1× length, frontal groove absent, POL:OOL:OCL 16:8:2. Antennae as in Figure 42.

Mesosoma: Mesoscutum with postero-medial alveoli moderate, surface appearing

shiny. Scutellum slightly longer than wide, evenly alveolate. Posterior margin of metanotum overlapping anterior propodeum. Propodeum mostly smooth laterad of median carina occasionally with light alutacous or alveolate sculpture, callus with 2 large setae and about 10 smaller ones.

Metasoma: Petiole wider than long, smooth. Metasoma 2.2–2.5× as long as wide, posterior margin of T2 straight, lateral surface smooth except for a small, alutaceous, setose area at antero-dorsal edge of each tergum.

Legs and wings: Foretibia with 2 longitudinal light stripes, without a curved spine at apex. Forewing hyaline, approximately 2.1× as long as broad, densely setose, marginal fringe present. Basal and cubital vein setae absent under submarginal vein, few subcubital setae present, ratio submarginal : marginal : stigmal : postmarginal 33: 47:5:5. Marginal vein not swollen at base.

Male. Unknown.

Host. Unknown.

Distribution. Known only from the type locality, Ontario.

Types. Holotype ♀ on point with data: "Ontario, Oxford Mills, 26-VI-1974. Collector, L. Masner" (Deposited in CNC, type no. 19576). Paratypes: 5♀♀, same data as holotype; 1♀, same locality as holotype, but collected 26-V-1975; 1♀, Ontario, Jockvale, 25-V-1951. O. Peck, swept from basswood. (CNC except 2 in USNM).

Etymology. This species is named in honor of O. Peck, well known chalcidologist who collected some of the type specimens.

Entedon procerus, new species
Fig. 41

Diagnosis. Foretibia without longitudinal stripes, metasoma 3.2–3.4× as long as wide; frontal grooves absent; interscrobes smooth; propodeum smooth laterad of median carina; all funiculars longer than wide (Fig. 41); toruli inserted above ventral margin of eye; eye height 2.7× malar space; dorsal head width 3.0× length.

This species is easily separated from other species with a black body by the elongate metasoma (metasoma no more than 2.2× length in *robustus, bigeloviae,* and *pecki*). The smooth or very lightly sculptured propodeum sets *procerus* apart from *leucopus* and *anthonomi.*

Description. Female. Length 2.7–2.9 mm. Color black except the following: some metallic dark blue reflections on the scape, dorsum of the thorax, propodeum, and T2. Mandibles, femora except at apex, foretibia except at base and apex, basal half of mid and hindtibia black to dark brown. Fourth tarsomere of all legs brown. Tips of femora, apex of foretibia, apical half of mid and hindtibia, first three tarsomeres of all legs yellow.

Head: Mandibles not enlarged, teeth subequal in length. Clypeus truncate, oral fossa 2.0× malar space. Interscrobes smooth, space between toruli alutaceous. Toruli inserted above ventral margin of eye, mid facial alveoli moderate in size, about 8–9 between midline and margin of eye. Interocular distance 3.0× width of eye, eye height 2.7× malar space. Head width in dorsal view 3.0× length, frontal groove absent, POL : OOL : OCL 13:5:3. Antennae as in Figure 41.

Mesosoma: Mesoscutum with postero-medial alveoli moderate in size, surface

shiny in appearance. Scutellum slightly longer than wide, medially with a few elongate alveoli at anterior edge. Posterior margin of metanotum overlapping anterior propodeum. Propodeum smooth laterad of median carina, callus with 2 large setae and 4–6 smaller ones.

Metasoma: Petiole (T1) wider than long, smooth. Metasoma 3.2–3.4× as long as wide, posterior margin of T2 straight, lateral surface smooth except for a small, alutaceous, setose area at antero-dorsal edge of each tergum.

Legs and wings: Foretibia without longitudinal light stripes, without a curved spine at apex. Forewing hyaline, approximately 2.3× as long as broad, densely setose, marginal fringe present. Basal and cubital vein setae absent under submarginal vein, ratio submarginal:marginal:stigmal:postmarginal 22:27:2:3. Marginal vein not swollen at base.

Male. Unknown.

Hosts. Unknown.

Distribution. Known only from Maryland and New York.

Types. Holotype ♀ on point with data: "MARYLAND, Plummers Island, 28-V-1911. J. C. Crawford Collector" (Deposited in USNM). Paratypes as follows: 1♀ with same data as holotype (USNM); 2♀♀, Laurel, Patuxent Wildlife Center, 4-VI-1981, L. Masner, Sweeping (CNC). NEW YORK, 1♀. Rome, June 24, 1934. H. K. Townes (AEI). 1♀, Long Island, New Haven, 22-VII-1974. M. Kamran (AMNH).

Etymology. The species epithet is from the Latin *procerus,* meaning long or slender and refers to the elongate metasoma of this species.

<center>

Entedon robustus (Crawford)
Figs. 21, 24, 43, 54
</center>

Eriglyptus robustus Crawford, 1907:180.
Entedon robustus (Crawford). Girault, 1916a.

Diagnosis. Frontal grooves absent; interscrobes smooth; malar space about ¼ eye height (Fig. 21); dorsal head width 3.1–3.1× length; foretibia without longitudinal stripes; F2 and 3 longer than wide (Fig. 43); metasoma about 2–2.2× as long as wide; forewing (Fig. 24) sparsely setose, bare under basal submarginal. Body black with dark blue or purplish metallic reflections, length about 2.2–2.4 mm.

Males with malar space ⅕ eye height. Interocular distance 2× eye width. Antenna as in Fig. 54. Metasoma about 2× as long as wide, with large basal yellow spot.

This species is most similar to *bigeloviae, genei,* and *pecki* which have a similar habitus with the metasoma about 2× as long as wide, body mostly black, and length about 2 mm (2.5–3 mm in *genei*). The presence of foretibial stripes readily separates *pecki.* F1 is 3× as long as wide in *genei* (Fig. 39) and the area between the toruli is smooth. The forewing is much more densely setose in *bigeloviae* (Fig. 23), the dorsal head width is 2.4× length and F 2 and 3 are subquadrate (Fig. 35).

Hosts. Coleoptera, Curculionidae: *Anthonomus nigrinus* Boheman.

Distribution. Southern and Southeastern U.S.

Types. Lectotype ♀ (present designation) on point with data: "Washington, D.C. VII-3-1906. P.1906.806.V.I.a 7/10. Par. *Anthon. nigrinus.* Hunter no. 1327." Type ♀. USNM no. 10045. *Eriglyptus robustus* Cwfd. 2♀♀, 1♂ paralectotypes with same data (all USNM). The lectotype ♀ is missing one antenna, one fore and hindwing,

and a hindleg. A head of one of the paralectotype females was slide mounted by Girault and is badly crushed. A fore and hind wing of the third female were slide mounted by the author.

Notes. Length varies from 1.9 mm (males) to 2.8 mm (females). There is often a distinct purple coloration to the head, side lobes of the mesoscutum, propodeum, and femora.

Other specimens examined. UNITED STATES. LOUISIANA. 7♀♀, 2♂♂, Tallulah, 7-5 & 8-19, 1909, bred from *Solanum carolinense,* Par. *Anthonomus nigrinus* (USNM). MISSOURI. 2♀♀, Boone Co., Columbia, Sept. 9, 1964; 7♀♀, same locality, 9 Dec., 1967 (USNM). NORTH CAROLINA. 1♀, Raleigh 4-VIII-1940 (USNM). VIRGINIA. 1♀, Louisa Co., 4 mi. S. Cuckoo, 1-VI-1985. Malaise; 1♀, Vienna, 9-7-1911, Parasite of *Anthonomus nigrinus* (USNM).

Entedon stephanopachi Heqvist
Figs. 30, 45

Entedon stephanopachi Heqvist, 1959:140.

Diagnosis. Frontal groove present (as in Fig. 12); scape 8× as long as wide, F1 4× as long as wide (Fig. 30); malar space ½ eye height; foretibia with longitudinal stripes; metasoma 3–4× as long as wide; mid and hind femora yellow except at base. Body length about 2.6 mm and color black.

The male of *stephanopachi* has the metasoma about 3× as long as wide and without a basal yellow spot, the mid and hindtibia are almost completely yellow with only a slight brown spot basally, and the antennae (Fig. 45) has all the funiculars longer than wide and the F5 is clearly separated from F4.

This species is most similar to *methion, ernobii,* and *washingtoni* which also have the frontal groove present. However, none of those species have foretibial stripes, and each has the mid and hindtibia dark except for the apex. This species may also be confused with *tachypterelli* which has the mid and hindtibia almost entirely yellow. However, that species lacks the frontal groove, the scape is about 6× as long as wide (Fig. 32), and F1 is 2–2.5× as long as wide.

Hosts. Coleoptera, Bostrichidae: *Stephanopachys substriatus* (Paykull) (as *pacificus* Casey), *S. rugosus* (Olivier). Scolytidae. *Dendroctonus ponderosae* Hopkins (mountain pine beetle). In Europe this species is recorded from an unidentified species of *Stephanopachys.*

Distribution. Oregon, California, North Carolina. Also occurs in Europe.

Types. Holotype ♀, on point with data: "Dal. Nos., 11/4/1959. B. Ehnstrom. *Stephanopachys* sp. Holotype *Entedon stephanopachi* ♀. K. J. Hedqvist" (SMNH). Examined.

Notes. No significant variation was observed in the few specimens available for study other than slight variation in length (2.3–2.8 mm), some of which is due to distortion of the metasoma.

Other specimens examined. UNITED STATES. CALIFORNIA. 1♀, Yosemite N.P., Summer 1970, *Dendroctonus ponderosae.* OREGON. 3♀♀, 1♂, Lambs mine, *Pinus ponderosae,* reared Dec. 5/14, *Stephanopachys pacificus,* Hopkins U.S. 12585 bx. NORTH CAROLINA. 1♀, Durham, reared, *Stephanop. rugosus,* 1293 (USNM).

Entedon tachypterelli Gahan
Figs. 32, 47

Entedon tachypterelli Gahan, 1931:38.

Diagnosis. Foretibia with 2 longitudinal stripes, midtibia with only basal ¼ to ⅓ brown, occasionally nearly entirely yellow, hindtibia with basal ¼ to ½ brown. Interscrobes smooth, frontal groove absent. F1 2× as long as wide (Fig. 32). Metasoma 3 to 3.3× as long as wide. This is a larger species with a body length of about 3.5–4 mm. Body color is generally purplish with some metallic blue green, except the metasoma which is black.

The males have the metasoma only 1.4× as long as broad. The malar space is narrow (⅕ eye height) and the oral fossa is 3× the malar space. The midtibia are entirely yellow except for a slight brown infuscation at the base. The hindtibia are light brown over the basal ⅓. Antennae as in Figure 47.

This species may be confused with *stephanopachi* which also has foretibial stripes, a long metasoma, and mostly yellow mid and hindtibia. However, *stephanopachi* has the frontal groove present and the antennal scape and F1 are longer (Fig. 30).

Hosts. Coleoptera, Curculionidae: *Tachypterellus concors cerasi* List; *T. quadrigibbus* (Say). There is a record of this species reared from *Coleophora* (Lepidoptera: Coleophoridae) that was cited as questionable on the label (see below). In view of the known host range of most of the species, I would regard that host association as probably erroneous.

Distribution. New York, North Carolina, Colorado, Ontario.

Types. Lectotype ♀ (present designation) on point with data: Colorado, G. M. List coll., 1927. ex. *Tachypterellus concors.* USNM type no. 43262. Gahan. Paralectotypes: 8♂♂ and 7♀♀ with same data as lectotype (USNM). Gahan stated in his original description that the specimens came from Ft. Collins.

Notes. The specimen from *T. quadrigibbus* is over 1.1 mm longer than the type series that was reared from *T. concors.* It has the sculpture on the propodeum stronger and the area of the nucha and the supracoxal flange are covered by stronger plicae. A female specimen from Canada has the midtibia almost entirely yellow. The foretibia of this species has the darkened area on the lateral surfaces reduced so that the yellow area is greater than the darker area. This is the opposite of the other species with foretibial stripes.

Other specimens examined. UNITED STATES. NEW YORK. 1♀, Champlain Valley, ex. *Tachypterellus 4-gibbus.* 1933. (USNM). NORTH CAROLINA. 1♀, L. Junalaska, 5-24-1954 (USNM). ONTARIO. 1♀, Marmora, 7-VI-1950, ex. *Crataegus* fruit, Host ? *Coleophora prunivora* (CNC).

Entedon teedoe, new species
Figs. 13, 28, 44

Diagnosis. Interscrobes alveolate, frontal groove absent; mid facial alveoli large, only 5 or 6 between eye and scrobe (Fig. 13); scape yellow or very light brown; foretibia with longitudinal stripes; mid and hindtibia yellow over at least half of length; F1 5× as long as wide (Fig. 28); metasoma 3× as long as wide, lateral surface of terga alutaceous. Large species, 4.7–5.2 mm and the thorax metallic green.

This species is most closely related to *ashmeadi* which shares the alveolate inter-scrobes and large mid facial alveolae, light colored scape, and evenly alutaceous metasomal terga. It can be separated by the length of the metasoma (only twice as long as wide in *ashmeadi*) and the length of F1 (only 3–4 × as long as wide in *ashmeadi* (Fig. 27)).

Description. Female. Length 4.7–5.2 mm. Color as follows: head, mesosoma, second metasomal tergum, coxae blue black to blue green. Rest of metasoma black or dark brown. Antennal pedicel and flagellum, mandibles, femora except dorsal apices, inner and outer lateral surface of foretibia, basal halves of mid and hind tibia dark brown. Scape, foretarsi and fourth mid and hind tarsomere light, yellowish brown. Anterior and posterior surface of foretibia, apices of mid and hindfemora, distal halves of mid and hindtibia, first 3 mid and hind tarsomeres, yellow.

Head: Mandibles with teeth subequal in length; clypeus truncate, oral fossa 2.5 × malar space. Interscrobes alveolate, without smooth area, space between toruli alu-taceous. Toruli inserted above ventral margin of eye, mid facial alveoli large, only 5–6 between midline and margin of eye. Interocular distance 2.8 × width of eye, eye height 3.1 × malar space. Head width in dorsal view 2.3 × length, frontal groove absent, POL : OOL : OCL 25:8:7. Antenna as in Figure 28.

Mesosoma: Mesoscutum with postero-medial alveoli moderate, surface shiny in appearance. Scutellum slightly longer than wide, medially with a line of elongate alveoli. Posterior margin of metanotum overlapping anterior propodeum. Propo-deum weakly sculptured laterad of median carina, callus with 2 large setae and 10–15 smaller setae.

Metasoma: Petiole (T1) wider than long, smooth. Metasoma 3.0–3.2 × as long as wide, posterior margin of T2 straight, lateral surface evenly alutaceous, not restricted to area around setae.

Legs and wings: Foretibia with 2 longitudinal light stripes, without a curved spine at apex. Forewing hyaline, 2.5 × as long as broad, densely setose, marginal fringe present. Basal and cubital vein setae absent under submarginal vein, ratio submar-ginal : marginal : stigmal : postmarginal 35:43:5:5. Marginal vein not swollen at base.

Male. Differs from the female by the following: scape (Fig. 44) black, 3 × as long as broad, F5 clearly separated from F4. Interscrobal area smooth, frontal groove indicated medially, not reaching margin of eyes. Mid-facial alveoli smaller, about 9 between eye margin and midline of face. Oral fossa 1.5 × malar space. Interocular distance 4 × width of eye, face along anterior margin of eye distinctly raised in side view. Midtibae almost entirely yellow, with only a slight brownish tinge at base. Hindtibia stained very light brown over basal ⅓. The only available male specimen is somewhat damaged with the forewings misshapen and the posterior metasoma missing.

Hosts. Coleoptera, Curculionidae: *Podapion gallicola* Riley.

Distribution. Ontario and New York.

Types. Holotype ♀ on point with data: "ONTARIO, Barry's Bay, 30-VI-1966. S66.1418.01. Host: *Apion gallicola*" (Deposited in CNC, type no. 19577). 1♀ paratype with data: "NEW YORK, Clarksville, June 22, 1956. J. A. Wilcox, collr., from gall of *Podapion gallicola*" (USNM). 1♀, 1♂, paratypes with data: "ONTARIO, Arnprior, 15-VI-36. F.I.S. ex. Podapion gall" (CNC).

Etymology. The species epithet is an arbitrary combination of letters.

Entedon washingtoni Girault
Figs. 22, 31

Entedon washingtoni Girault, 1917:109.

Diagnosis. Foretibia without stripes; frontal grooves present; metasoma 2× as long as wide, T2 excised medially (Fig. 22), forewing without cubital or basal vein setae (speculum open); antennae (Fig. 31) with scape 8× as long as wide, F1 4× as long as wide; midtibia with basal ½ brown, remainder yellow.

This species is most easily confused with *methion, stephanopachi,* and *ernobii* which also have the frontal grooves present. All of these other species have the metasoma more than 2× as long as wide and T2 is not excised medially. In addition, *ernobii* has the speculum closed (Fig. 25) and *stephanopachi* has foretibial stripes.

The head of this species has been badly crushed on a slide and it is not possible to assess accurately the malar space or width of the oral fossa.

Notes. The only known specimen is the holotype.

Hosts. Unknown.

Types. Holotype ♀ on point with data: "Washngtn [sic] D.C. Red tag with no 20436. *Entedon washingtoni* Gir. ♀ type." (USNM).

HOSTS OF NORTH AMERICAN *ENTEDON*

	Host	*Entedon* sp.
	Coleoptera	
Curculionidae	*Anthonomus signatus* Say	*anthonomi*
	A. nigrinus Boheman	*robustus*
	Epimechus sp.	*bigeloviae*
	Apion occidentale Fall	*columbianus*
	Podapion gallicola Riley	*teedoe*
	Tachypterellus concors cerasi List	*tachypterelli*
	T. quadrigibbus (Say)	*tachypterelli*
Scolytidae	*Scolytus multistriatus* (Marsham)	*ergias*
	S. rugulosus (Muller)	*ergias*
	Dendroctonus ponderosae Hopkins	*stephanopachi*
Anobiidae	*Ernobius pinicola* Ruckes	*ernobii*
	E. melanoventris Ruckes	*ernobii*
	E. mollis L.	*methion*
Bostrichidae	*Stephanopachys substriatus* (Paykull)	*stephanopachi*
	S. rugosus (Olivier)	*stephanopachi*
	Hymenoptera	
Tenthredinidae	*Euura exiguae* Smith	*columbianus*
	E. lasiolepis Smith	*columbianus*
	E. geyerianae Smith	*columbianus*
	Pontania sp.	*columbianus*

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A REVIEW OF THE GENUS *KROMBEINIUS* (HYMENOPTERA: PERILAMPIDAE) WITH A REEXAMINATION OF GENERIC LIMITS AND PHYLOGENETIC RELATIONSHIPS AND THE DESCRIPTIONS OF TWO NEW SPECIES

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Abstract.—The world species of *Krombeinius* are reviewed and two new species are described, *K. taiwanensis* from Taiwan and *K. srilanka* from Sri Lanka. A cladistic analysis strongly supports the monophyly of *Krombeinius* and *Euperilampus* and provides a phylogenetic hypothesis for the relationships of the species of *Krombeinius*.

In my earlier contributions to the systematics of *Krombeinius* and *Euperilampus* (Darling, 1983a, b) I noted that the genus *Krombeinius* was characterized by the absence of the synapomorphies of *Euperilampus,* by symplesiomorphy. As a solution, I proposed the unique configuration of the labrum as an autapomorphy of *Krombeinius,* based only on the type species *K. eumenidarum*. The recent description of a new species of *Krombeinius* from the Ethiopian region (Rasplus, 1987) and the discovery of additional undescribed Oriental species in collections have provided the opportunity to test this prediction. I have now been able to examine the labrum in two additional species of *Krombeinius* and the morphology is consistent with that hypothesis of monophyly. This additional material also provided the impetus to review the world species of *Krombeinius* and to investigate their phylogenetic relationships.

The referral of these new species to the genus *Krombeinius* was initially problematic and required a revised generic concept. The description and diagnosis of the genus are herein modified to a significant degree. The previous diagnosis was effectively a phenetic characterization which can now be replaced with a synapomorphy scheme. The result is a taxon based on a hypothesis of common ancestry that includes phenetically rather dissimilar species due to the differential retention of, and reversal to, primitive features.

Abbreviations used in the text: F1–7, funicular segments; MSC, length of mesoscutum along midline; OOL, length of ocular-ocellar line; PN, length of pronotum along midline; POL, length of posterior ocellar line; SC, length of scutellum along midline; T2–8, metasomal tergites 2–8. Figures are referred to by the convention: Fig., for figures in this paper and fig., for figures in previous publications. Sculpture types follow Eady (1968).

Krombeinius Bouček

Krombeinius Bouček, 1978:302, figs. 1, 2 [original description, key]; Darling, 1983a: 308, figs. 1, 2, 3, 6–17 [diagnosis, description, phylogenetic relationships]; Darling, 1983b:34, fig. 77 [phylogenetic relationships].

Type species: *Krombeinius eumenidarum* Bouček, 1978:302, fig. 1. [original designation]

Diagnosis. Moderately large (3 to 6 mm) and robust perilampids, black in color without metallic reflections (habitus drawing in Darling, 1983a), differentiated from other perilampid genera by the following combination of characters (apomorphies in bold face): marginal vein of forewing longer than postmarginal vein (Figs. 8, 14); **labrum with a central stalk,** lacking aboral digits (Fig. 4); **third metasomal tergite massive, much larger than second** (Darling, 1983a, fig. 1); and malar sulcus obliterated by oblique costae (Figs. 1, 2).

Description. Head: subequal in width to pronotum, in dorsal view transverse; supraclypeal area smoothly convex, without horn or ridge; scrobal cavity deep, extended to lower ocular line or to middle of clypeus; lower edge of antennal torulae above lower ocular line; clypeus and supraclypeal area separated by distinct suture or by faint line; inner orbits carinate and in some species developed as prominent scrobal walls, smooth or with distinct costae; frontal carina separating the median and posterior ocelli; malar sulcus absent; malar region with oblique costae; OOL/POL diagnostic; labiomaxillary complex short, maxillary palp 4-segmented, labial palp 3-segmented; labrum with a narrow central stalk, expanded distally with 7–10 short digits, each with a tapered seta, and with paired sessile setae not associated with digits.

Mesosoma: dorsum of pronotum smoothly convex, without transverse elevations; pronotum variable in size and shape; mesothoracic spiracle located between pronotum and sidelobe of mesoscutum; prepectus fused to the pronotum, width variable relative to adjacent pronotum, with many or a single fovea; notauli distinct and complete; scutellum vaulted, jutting over propodeum and base of metasoma; apex of scutellum acuminate, truncate or with a distinct spine; propodeum with median area foveate, or with a short median ridge, submedian areas with weak transverse rugae or aciculate; basitarsomere not conspicuously lengthened. Forewing with marginal vein longer than postmarginal, postmarginal vein long, about 2–3 times length of stigmal vein, stigmal vein making either 90° or oblique angle with marginal vein.

Metasoma: petiole short, transverse, the tergum forming a ridge along anterior face of gaster, sternum shifted posteriorly; T2 and T3 fused, covering most of dorsum; T3 massive and convex, about twice length of T2 along midline, length about equal to maximum width; ovipositor ventral, not upturned, sheaths not distinctly exserted; male genitalia with distinct parameres.

KEY TO THE SPECIES OF *KROMBEINIUS*

1.   Inner orbits with strong costae, extended from posterior ocelli to clypeus (Darling, 1983a, figs. 8, 9, 16, 17); pronotum, in lateral view, with distinct callus, giving the impression of bumpy shoulders (Darling, 1983a, fig. 1) 2
1'.   Inner orbits smooth, without strong costae (Figs. 1, 2, 10, 11); pronotum without distinct callus (Fig. 13), if callus weakly developed (Fig. 6) then head, in lateral view, without inner orbits developed as prominent scrobal walls (Fig. 2) 3
2(1).   Apex of scutellum with prominent spine (Darling, 1983a, figs. 1, 15) [Philippines] .... *K. saunion*
2'(1). Apex of scutellum truncate, not produced as a prominent spine (Figs. 5, 6, 12, 13) [Southern India, Sri Lanka] .... *K. eumenidarum*

3(1′). Third metasomal tergite (T3) finely and densely punctulate; malar region with very weak and short costae (Figs. 10, 11) [Sri Lanka] .... *K. srilanka,* n. sp.

3′(1′). Third metasomal tergite (T3) smooth, without impressed surface sculpture; malar region with distinct oblique costae (Figs. 1, 2) 4

4(3′). Prepectus with single fovea (Bouček, 1978, fig. 2); propodeum and metanotum subequal in length [Malaysia, Sarawak] .... *K. megalaspis*

4′(3′). Prepectus with many foveae (Fig. 7); propodeum about twice length of metanotum 5

5(4′). Head, in lateral view, broad, inner orbits developed as prominent scrobal walls (as in Fig. 10); scutellum, in lateral view, evenly convex, gradually tapered toward apex (Rasplus, 1987, fig. 1) [West Africa] .... *K. lerouxi*

5′(4′). Head, in lateral view, narrow, inner orbits not developed as prominent scrobal walls (Fig. 2); scutellum, in lateral view, vaulted, not gradually tapered toward apex (Fig. 6) [Taiwan] .... *K. taiwanensis,* n. sp.

SYNOPSIS OF THE WORLD SPECIES OF *KROMBEINIUS*

Krombeinius eumenidarum Bouček
Fig. 17

Krombeinius eumenidarum Bouček, 1978:302, fig. 1; Darling, 1983a, figs. 2, 3, 6–9 [male genitalia, labrum, phylogenetic relationships].

Distribution. Sri Lanka, India.

Diagnosis. This species can be distinguished by the combination of costate inner orbits and truncate scutellum, not produced as an elongate spine as in *K. saunion* (Darling, 1983a, fig. 15). This species can be further distinguished from its sympatric congener, *K. srilanka,* by the more massive scrobal walls with distinct costae (Darling, 1983a, fig. 17; cf. Fig. 10) and much larger pronotum, in dorsal view one-third length of mesoscutum *versus* one-fifth (Darling, 1983a, fig. 15; cf. Fig. 12) and smaller prepectus, in lateral view about one-third width of adjacent pronotum *versus* about one-half (Darling, 1983a, fig. 1; cf. Fig. 13).

Host. This species is a primary parasitoid of *Paraleptomenes mephitis* (Cameron) [Vespidae: Eumeninae] (see Krombein, 1978).

Krombeinius megalaspis (Cameron)

Perilampus megalaspis Cameron, 1912:63; Bouček, 1978, fig. 2 [lectotype designation, n. comb.]; Darling, 1983a, figs. 10–13 [phylogenetic relationships].

Distribution. Malaysia, Sarawak.

Diagnosis. Only this species and *K. lerouxi* have the inner orbits smooth but still developed as prominent scrobal walls. These species may be distinguished by the relative sizes of the propodeum and metanotum; subequal in length in *K. megalaspis* and the metanotum is only about one-half length of propodeum in *K. lerouxi.* In addition, the pronotum in lateral view is regularily convex in *K. megalaspis,* without the raised callus which gives the suggestion of bumpy shoulders in specimens of *K. lerouxi* (as in Fig. 6).

Notes. In my earlier discussion of the genus I noted that this species was problematic in many regards and that a revised classification might necessitate a new monobasic

genus. The cladogram (Fig. 19) suggests that this species may be the sister group to the other species of the genus. Known only from the type material.

Krombeinius saunion Darling

Krombeinius saunion Darling, 1983a:313, figs. 1, 14–17 [phylogenetic relationships].

Distribution. Philippines, Mindanao.

Diagnosis. This is the only species of the genus with the apex of scutellum produced as a prominent spine. In other characters the species is quite similar to *K. eumenidarum* (additional distinguishing features are presented in Darling, 1983a).

Notes. The name of this species was inadvertently spelled in two ways in the original publication. Following the Principle of the First Reviser [ICZN 1983, Articles 24 and 32 (b)(i)], the above name is here chosen as the correct original spelling. Known only from the holotype.

Krombeinius lerouxi Rasplus
Fig. 15

Krombeinius lerouxi Rasplus, 1987:9, figs. 1–3.

Distribution. West Africa (Ivory Coast, Cameroon).

Diagnosis. This species and *K. megalaspis* are the only species in which the stigmal vein makes an oblique angle with the marginal vein (Rasplus, 1987, fig. 3). In all other species this angle is approximately 90° (Figs. 8, 14). These two species can be distinguished by the relative sizes of the propodeum and metanotum (see "Diagnosis" of *K. megalaspis*). The male of *K. lerouxi* has infumate wings in the region surrounding the sitgmal vein and a distinctive pattern of punctures on the surface of the male scape (Fig. 15).

Redescription. Female: Length, about 6 mm. Black, except tegula and mandible reddish-brown, foretibial spur and tarsi yellow; wings hyaline, veins darkened.

Head (Rasplus 1987, figs. 1, 2): wider than pronotum, in dorsal view transverse, width : length = 1.92; in frontal view transverse, width : height = 1.16; maximum width of scrobe 0.52 head width; frontal carina extended below lower ocular line, convergent on clypeus; length of malar space 0.22 eye height; OOL 0.95 POL; inner orbits smooth and shining, developed as prominent scrobal walls; outer orbits costate, convergent on clypeus (Fig. 1); scrobal cavity deep and broad, delimited by frontal carina, extended to lower ocular line; clypeus transverse, width : height = 1.50, polished and sparsely covered with setae, longer and denser along margin; clypeus delimited by weak sutures and with raised median callus, upper margin indicated by faint line, lower margin strongly emarginate; tentorial pits indistinct; supraclypeal area glabrous, height 0.52 clypeus height, convex along midline, laterad with distinct channels for reception of antennae; ocular-ocellar region smooth and shining without costae radiating from ocelli; vertex with strong costae at posterior margin. Labrum with 8–10 very short subsessile digits and strongly excised medially (inverted Y-shape, much more strongly excised than in *K. taiwanensis,* Fig. 4 and *K. eumenidarum,* Darling, 1983a, fig. 3). Antenna: scape narrowly linear, length about 7.3 maximum width; pedicel and funicular segments (F1–F7) subequal in length (17

versus 14, 14, 15, 14, 14, 11, 13); pedicel 0.21 scape length; annellus 0.32 length of F1; F1–F7 transverse, wider than long; clava 0.38 length of funicle.

Mesosoma (Rasplus, 1987, fig. 1): pronotum massive, PN:MSC = 0.26, as in *Perilampus,* lateral pronotum rounded, with only a slight suggestion of bumpy shoulders; scutellum acuminate, SC:MSC = 1.23; dorsum of pronotum, midlobe of mesoscutum, and scutellum punctate-reticulate, coalesced to form weak transverse costulae medially; sidelobes of mesoscutum smooth along notauli, laterally punctate; scutellum in lateral view not strongly convex; underside of scutellum smooth, with shallow convergent grooves; median area of propodeum foveate, about twice as long as metanotum (49:28), submedian areas delimited by lateral ridges, with transverse costulae, callus not raised, on the same plane as submedian areas, coriarious; width of prepectus 0.49 width of adjacent pronotum, with about 8 foveae, sculpture differentiated from adjacent pronotum by narrow glabrous area; axilla punctate-reticulate above, smooth below, without distinct costae; axillula triangular and not extended towards apex of scutellum as fingerlike lobe, without distinct crenulae. Forewing venation (Rasplus, 1987, fig. 3): submarginal vein 2.6 marginal vein, postmarginal 0.57 marginal, stigmal 0.26 marginal, stigmal 0.46 postmarginal, stigmal vein making oblique angle (125°) with marginal vein, stigma expanded below, with 3 or 4 sensilla.

Metasoma: T2 smoothly concave with sparse setae concentrated at posterolateral margin, without punctures, laterotergite glabrous; border between T2 and T3 indicated by sinuous suture; dorsal surface of T3 evenly covered with short setae except along T2 border and along margins of tergite, without distinct punctures; ovipositor not examined.

Male: Differs from female only in following regards: forewing infuscate in region surrounding stigmal vein; clypeus with many more setae; scape, in frontal view, expanded apically with punctures distributed in a distinct V-shaped pattern (Fig. 15).

Notes. This redescription is based on the holotype female (Museum National d'Histoire Naturelle, Paris) and a recently collected topotypic male specimen. The host of this species is unknown but paratypes were reared from tree branches. As noted by Rasplus (1987), it is certainly possible that the branches contained nests of eumenine vespids.

<div align="center">

Krombeinius taiwanensis, new species

Figs. 1–8

</div>

Type locality. Taiwan.

Type material. "Kurario [?] Formosa Gressitt [collector]," handwritten; Slide #595–596 D. Chris Darling, labrum, labiomaxillary complex; Holotype ♀ *Krombeinius taiwanensis* D. Chris Darling '88. The specimen was remounted on cards after dissection of the mouthparts. The body is on the top card with the head detached. The lower card has the original paper point, with midlegs still attached, and the antennae; the specimen is otherwise in excellent condition. The mouthparts are slide-mounted in Canada Balsam.

Type repository. Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.

Etymology. The specific epithet is a reference to the type locality.

Diagnosis. This species can be recognized immediately as the only member of the genus without the inner orbits developed as prominent scrobal walls, the head in
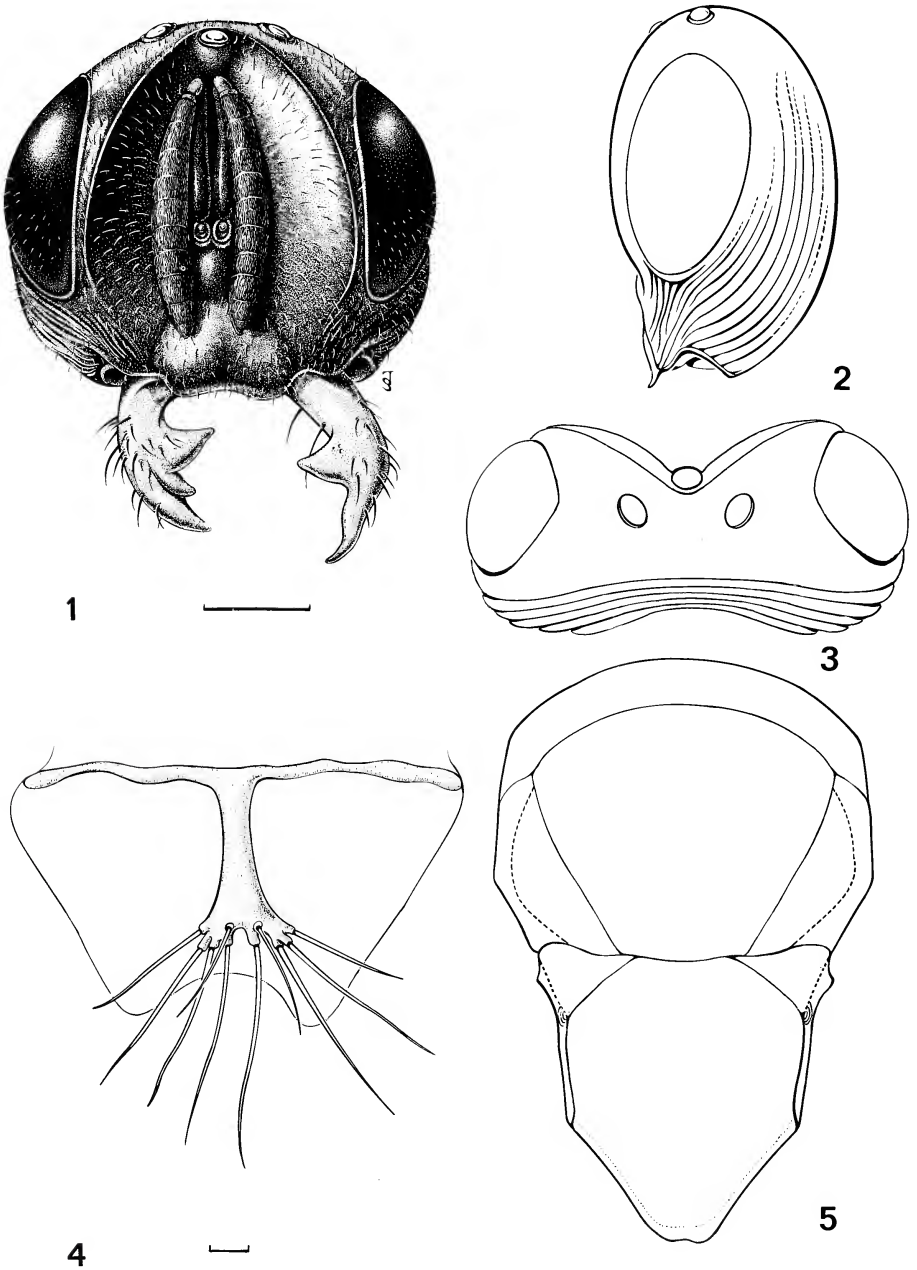
Figs. 1–5.   *Krombeinius taiwanensis,* new species. 1. Head, frontal. 2. Head, lateral. 3. Head, dorsal. 4. Labrum and epipharynx. 5. Mesosoma, dorsal; dashed line indicates extent of smooth areas along notauli and on axillae. Figs. 1–3, 5 drawn to same scale, scale line 0.5 mm; Fig. 4, scale line 0.05 mm.

lateral view is narrowly convex (Fig. 2; cf. Fig. 10 and figs. 9, 13, and 17 in Darling, 1983a). This species and *K. srilanka* share a number of similarities. In both species, the prepectus is much wider than in all other species, greater than one-half the width of the adjacent pronotum *versus* approximately 0.45 in all other species (Fig. 6; cf. fig. 1 in Darling, 1983a and figs. 1, 2 in Bouček, 1978) and the pronotum is narrow in dorsal view, 0.2 the length of the mesoscutum *versus* 0.30–0.35 (Fig. 5; cf. figs. 7, 11, and 15 in Darling, 1983a). The strong costae in the malar region will distinguish these two species (Fig. 2; cf. Fig. 10).

Description. Female: Length, 5 mm. Black, except tegula and flagellum brown, mandible reddish-brown, apex of foretibia and spur, and tarsi yellow; wings hyaline, veins darkened.

Head (Figs. 1–3): wider than pronotum, in dorsal view transverse, width : length = 1.97; in frontal view transverse, width : height = 1.12; maximum width of scrobe 0.64 head width; frontal carina extended below lower ocular line; length of malar space 0.31 eye height; OOL 0.94 POL; inner orbits smooth and shining, not developed as prominent scrobal walls; outer orbits with costae convergent on clypeus (Fig. 1); scrobal cavity deep and broad, delimited by frontal carina, extended to lower ocular line; clypeus transverse, width : height = 1.40, polished and sparsely covered with setae, longer and denser along margin; clypeus delimited by weak sutures and with raised median callus, upper margin indicated by faint line, lower margin strongly emarginate (Fig. 1); tentorial pits indistinct; supraclypeal area glabrous, height 0.68 clypeus height, convex along midline, laterad with distinct channels for reception of antennae; lower edge of antennal torulae above lower ocular line; ocular-ocellar region smooth and shining without costae radiating from ocelli (Fig. 3); vertex with strong costae at posterior margin. Labrum (Fig. 4): with 8 very short subsessile digits and not strongly excised medially (cf. *K. eumenidarum,* Darling 1983a, fig. 3). Antenna: scape narrowly linear, length about 8.5 maximum width; pedicel and funicular segments (F1–F7) subequal in length (17 *versus* 12, 12, 14, 13, 14, 14, 12); pedicel 0.26 scape length; annellus 0.41 length of F1; F1–F7 transverse, wider than long; clava 0.38 length of funicle.

Mesosoma (Figs. 5–7): pronotum not massive, PN:MSC = 0.19, as in *Perilampus,* lateral pronotum convex, with only slight suggestion of bumpy shoulders, much less distinct than in *K. eumenidarum*; scutellum truncate (Fig. 5), SC:MSC = 1.12; dorsum of pronotum, midlobe of mesoscutum, and scutellum punctate-reticulate; sidelobes of mesoscutum smooth along notauli, laterally punctate-reticulate; scutellum in lateral view strongly convex, apex high, subvertical (Fig. 6); underside of scutellum smooth, with shallow convergent grooves; median area of propodeum with deep crenulate groove along anterior margin and median ridge about twice as long as metanotum (49:28), submedian areas distinctly delimited by median and lateral ridges, with transverse costulae, callus reticulate-rugose; width of prepectus 0.60 width of adjacent pronotum (Fig. 6), with about 20 foveae (Fig. 7), sculpture undifferentiated from adjacent pronotum; axilla punctate-reticulate above, costulate below; axillula large and distinctly separated from scutellum and extended towards apex of scutellum as fingerlike lobe (Fig. 6), smooth except for weak crenulae ventrad. Forewing venation (Fig. 8): submarginal vein 2.9 marginal vein, postmarginal 0.62 marginal, stigmal 0.26 marginal, stigmal 0.43 postmarginal, stigmal vein making slightly oblique angle with marginal vein, stigma rounded with 4 sensilla.
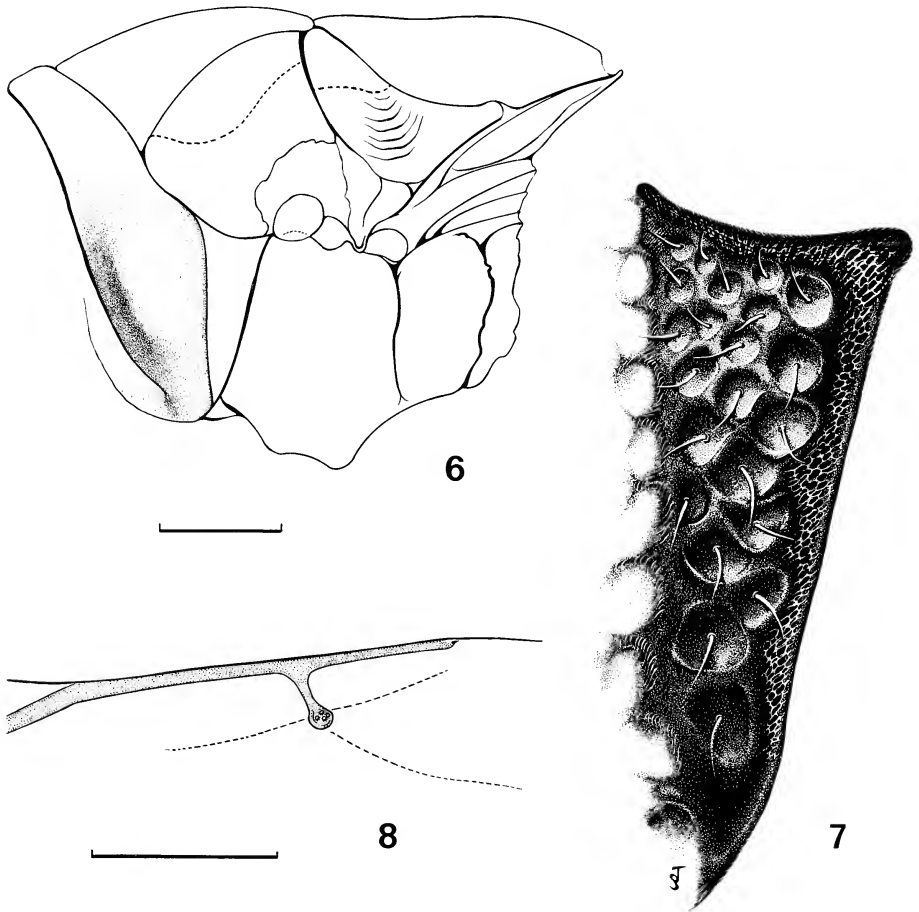
Figs. 6–8. *Krombeinius taiwanensis,* new species. 6. Mesosoma, lateral view. 7. Prepectus. 8. Forewing venation. Scale lines, 0.5 mm.

Metasoma: T2 smoothly concave with sparse setae, without punctures, laterotergite glabrous; border between T2 and T3 indicated by sinuous suture; T3 smooth and shining, evenly covered with short setae except along T2 border and along margins of tergite, with distinct but small punctures laterad; ovipositor not examined.

Male: Unknown.

Krombeinius srilanka, new species
Figs. 9–14, 16

Type locality. Trincomalee, Sri Lanka.

Type material. "Sri Lanka: Tri. Dist. Trincomalee, China Bay Ridge Bungalow 0-100'," "Adult eclosed 2 Aug 1978 K. V. Krombein," "Host: *Paraleptomenes mephitis*

(Sauss.)," "Holotype ♂ *Krombeinius srilanka* D. Chris Darling '88." The specimen is point-mounted and in excellent condition.

Type repository. United States National Museum, Washington, DC, U.S.A.

Etymology. The specific epithet is a noun in apposition, a reference to the type locality.

Diagnosis. This is the only species in the genus with distinct sculpture covering the majority of the surface of either T2 or T3; both sclerites are sculptured in this species. In addition, *K. srilanka* differs from all other species by having fewer and weaker costae in the malar region (Fig. 10; cf. Fig. 2) and having the lateral ocelli situated much closer to the eyes than the anterior ocellus, OOL about one-half POL *versus* OOL = POL (Fig. 9; cf. Fig. 3). Additional characters to distinguish this species and its sympatric congener, *K. eumenidarum,* include smooth inner orbits *versus* costate (Fig. 10; cf. fig. 9 in Darling, 1983b) and the pattern and distribution of punctures on the male scape (Fig. 16; cf. Fig. 17). See also "Diagnosis" of *K. eumenidarum.*

Description. Male: Length, 3.5 mm. Black, except flagellum brown, mandible reddish-brown, tegula, apex of foretibia and spur, and tarsi yellow; wings hyaline, veins darkened.

Head (Figs. 9–11): wider than pronotum, in dorsal view transverse, width : length = 2.0; in frontal view transverse, width : height = 1.15; maximum width of scrobe 0.63 head width; frontal carina not reaching lower ocular line; length of malar space 0.20 eye height; posterior ocelli closer to eyes than in other species (Fig. 9), OOL 0.51 POL; inner orbits smooth and shining, developed as low scrobal walls (Fig. 10); outer orbits smooth without distinct costae (Figs. 10–11); scrobal cavity deep and narrow, not delimited by frontal carina, extended to lower ocular line; region between frontal carina and scrobal declivity with long and dense white setae; clypeus transverse, width : height = 1.74, polished and sparsely covered with setae, longer and denser along margin; clypeus delimited by weak sutures and without median callus, upper margin indicated by distinct suture, lower margin strongly emarginate (Fig. 11); tentorial pits indistinct; supraclypeal area glabrous, height 0.65 clypeus height, convex along midline, without distinct channels for reception of antennae; ocular-ocellar region smooth and shining without costae radiating from ocelli (Fig. 9); vertex with strong costae at posterior margin. Labrum not examined. Antenna: scape length about 4.8 maximum width; flagellum long, reaching anterior margin of clypeus; pedicel and funicular segments (F1–F7) subequal in length (10 *versus* 14, 11, 12, 13, 13, 12, 11); pedicel 0.24 scape length; annellus small, 0.21 length of F1; F1–F7 transverse, wider than long; clava 0.24 length of funicle; scape, in frontal view, expanded only slightly apically with punctures distributed as in Fig. 16.

Mesosoma (Figs. 12, 13): pronotum not massive, PN:MSC = 0.20, lateral pronotum flat, without any suggestion of bumpy shoulders; scutellum truncate, with crenulate margin but not completely delimited by distinct carina, SC:MSC = 1.23; dorsum of pronotum, midlobe of mesoscutum, and scutellum punctate-reticulate, punctures not coalesced to form transverse costulae medially; sidelobes of mesoscutum smooth along notauli, laterally punctate; scutellum in lateral view convex (Fig. 13); underside of scutellum roughened, without convergent grooves; propodeum with distinct median ridge, submedian areas with transverse costae, medially about twice as long as metanotum (35:17), submedian areas delimited by median and lateral ridges, with
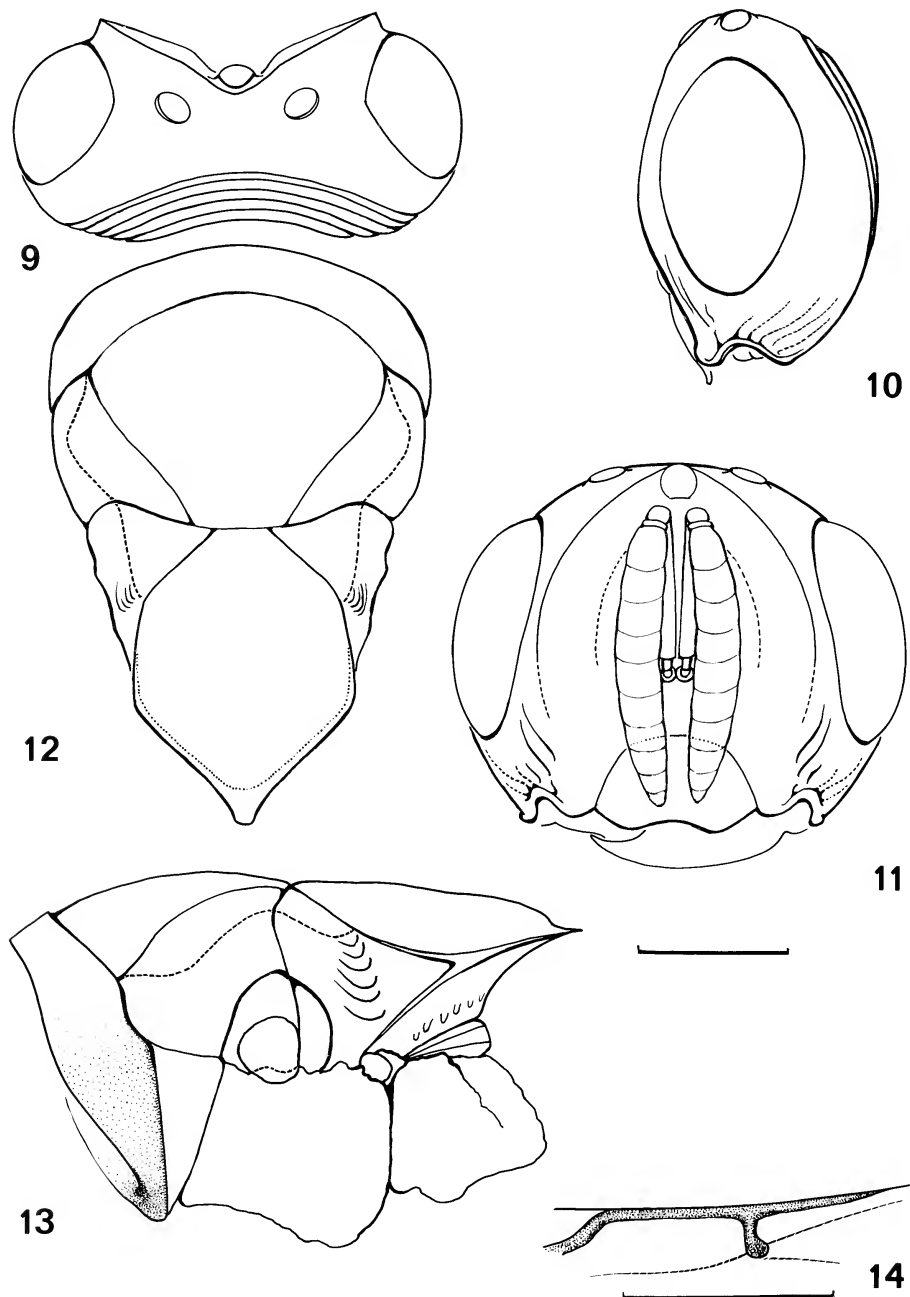
Figs. 9–14.   *Krombeinius srilanka,* new species. 9. Head, dorsal. 10. Head, lateral. 11. Head, frontal. 12. Mesosoma, dorsal; dashed line indicates extent of smooth areas along notauli and on axillae. 13. Mesosoma, lateral. 14. Forewing venation. Figs. 9–13 drawn to same scale, scale line 0.5 mm; Fig. 14, scale line 0.05 mm.
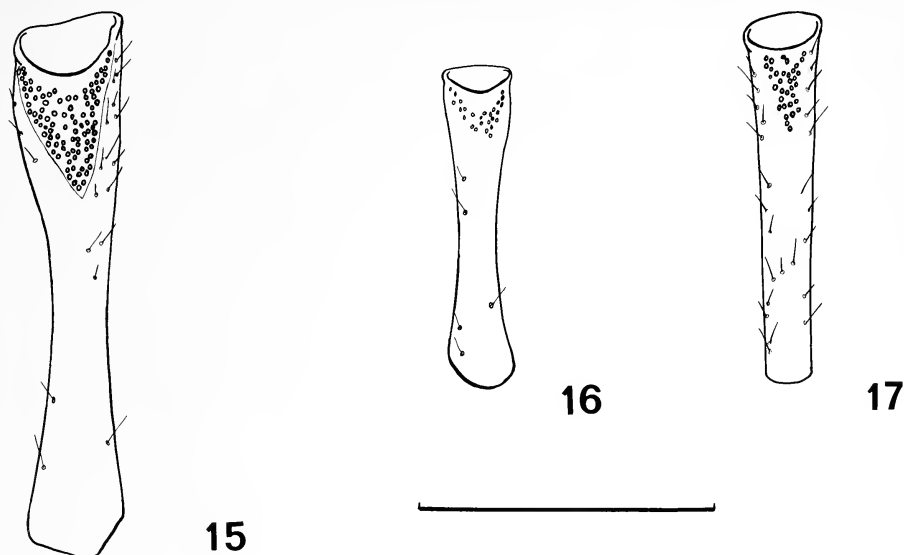
Figs. 15–17. *Krombeinius* species, male scapes. 15. *K. lerouxi.* 16. *K. srilanka.* 17. *K. eumenidarum.* Scale line, 0.5 mm.

transverse costulae, callus large and raised, reticulate-rugose; width of prepectus 0.55 width of adjacent pronotum (Fig. 13), with about 16 foveae, differentiated from adjacent pronotum by narrow glabrous area; axilla punctate-reticulate above, costulate below; axillula triangular, not extended towards apex of scutellum as fingerlike lobe, smooth except for weak crenulae ventrad. Forewing venation (Fig. 14): submarginal vein 3.4 marginal vein, postmarginal 0.74 marginal, stigmal 0.24 marginal, stigmal 0.33 postmarginal, stigmal vein making slightly oblique angle with marginal vein, stigma rounded with 4 sensilla.

Metasoma: T2 concave with distinct groove along midline, aciculate with setae only at the posterolateral margin, without punctures; basal fovea distinct and transverse; laterotergite glabrous; border between T2 and T3 indicated by sinuous suture; T3 finely reticulate-coriarious, evenly covered with long setae except along T2 border and along margins of tergite.

Female: Unknown.

Host. This species is a primary parasitoid of *Paraleptomenes mephitis* (Cameron) [Vespidae: Eumeninae].

Notes. It is somewhat disconcerting that this species is sympatric with *K. eumenidarum* and also attacks the same species of potter wasp. Initially, consideration was given to broadening the concept of *K. eumenidarum* to include this specimen. A male specimen was available for comparison (India, Kerala, length 4.2 mm). As discussed in the diagnosis, these species are quite different in morphology; furthermore, the phylogenetic analysis suggests that these sympatric species are only distantly related within the genus. The number and distribution of punctures on the male scape supports the hypothesis that two distinct species are involved. The male scape has

proven to be of considerable value in distinguishing species in other perilampid genera (e.g., *Euperilampus,* Darling, 1983b) and the hypothesized sister group of the Perilampidae, the Chrysolampinae (Darling, 1986).

A phylogenetic analysis was conducted to refine the previous cladogram presented for the derived elements of the Perilampidae (Darling, 1983b). The monophyly of *Krombeinius* + *Euperilampus* needed to be reconsidered in light of the unique combinations of characters exhibited by *K. taiwanensis* and *K. srilanka.* The genera were previously related on the basis of four synapomorphies, all of which are now suspect. The second goal was to test the monophyly of the traditional genera, *Euperilampus* and *Krombeinius.* Finally, intrageneric relationships were investigated for the six species of *Krombeinius.*

Character polarity was initially determined using the *Perilampus hyalinus* species group as the outgroup, based on a sister group relationship between this species group and *Euperilampus* + *Krombeinius* (Darling, 1983b). The *Euperilampus scutellatus* species group was included to represent the groundplan characters for this genus. Twenty-three characters were coded for the eight taxa (Table 1). Parsimony analyses were conducted using the PAUP program (David Swofford, Illinois Natural History Survey). The small number of taxa allowed the use of the ALLTREES option, guaranteeing the shortest tree(s), and the BBSAVE = x option, to determine how many trees were only slightly longer than the shortest possible tree. The UNORDERED option was used to investigate possible codings for multistate characters and the DELCHAR option was used to investigate the influence of individual characters on the shortest trees. Strict consensus trees were constructed using the CONTREE program in the PAUP package.

Character 1. The sculpture of the inner orbits exhibits diverse configurations in the Perilampidae. In *Burksilampus, Steffanolampus,* and all plesiomorphic species groups of *Perilampus* the inner orbits are smooth or impunctate. Distinct raised rugae or costae are found only in the *Perilampus hyalinus* group, *Euperilampus,* and *Krombeinius.* However, smooth or impunctate sculpture is also found in all three groups. I previously interpreted costate inner orbits as a synapomorphy of *Euperilampus* + *Krombeinius* (Darling, 1983b, character 13). An equally parsimonious interpretation is that this character is synapomorphic at the level of *P. hyalinus* group + (*Euperilampus* + *Krombeinius*). I have coded costate inner orbits as plesiomorphic (state 0) and regard smooth or impunctate inner orbits as derived (state 1) in *Krombeinius*; a similar reversal to a phenotypically plesiomorphic condition is evident in *Euperilampus* (Darling, 1983b). The cladogram (Fig. 19) suggests that the common ancestor of *Krombeinius* species had smooth inner orbits and that the costate inner orbits of *K. eumenidarum* + *K. saunion* and *Euperilampus* species are a result of convergence, not the retention of an ancestral character.

Character 2. In the initial analysis multiple characters were coded that dealt with the configuration of the pronotum and prepectus. In my earlier study (Darling, 1983b) I recognized two characters, width of prepectus (character 3) and size of pronotum in dorsal view (character 12). In this study I initially added a third character, the shape of the pronotum in dorsal view. In each analysis homoplasy was present in each of the three characters and the extra steps in each character occurred at the

Table 1. Character states for 23 characters and 8 taxa included in the cladistic analysis (0 = ancestral state; 1, 2, 3 = derived states; ? = missing data). See text for discussion of character polarity and transformation series.

Taxon	Characters

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
*Perilampus hyalinus group	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euperilampus scutellatus group	0	3	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1	0	1
Krombeinius megalaspis	1	2	0	?	?	?	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	1	0
Krombeinius eumenidarum	0	2	0	1	0	1	1	0	0	1	2	0	0	0	0	1	0	0	1	1	0	1	0
Krombeinius saunion	0	2	0	?	?	?	1	0	0	1	2	0	0	0	0	0	0	1	0	1	0	1	0
Krombeinius taiwanensis	1	1	1	1	0	1	1	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0
Krombeinius lerouxi	1	2	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
Krombeinius srilanka	1	1	0	?	?	?	1	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0

same internodes on each of the cladograms. After further consideration it was obvious that a suite of morphological attributes is associated with a tendency towards either an elongation or a shortening of the mesosoma. The prepectus is fused to the pronotum and bridges the gap between the lateral pronotum and the mesopleuron. These three characters provide no unique information and are different ways of describing the same morphological relationship. The multiple manifestations of the pronotum/prepectus correlation had confounded the search for parsimonious cladograms and my solution was to code only a single character. This character is a multistate character with four states (Fig. 18). In the outgroup and in all species of *Perilampus*, the prepectus is broader than the adjacent pronotum (state 0). In all species of *Euperilampus* the prepectus is very narrow, less than one-fifth the width of the adjacent pronotum (state 3). Neither of these states are found in *Krombeinius*; the prepectus is intermediate in size. In *K. eumenidarum, saunion, lerouxi,* and *megalaspis* the pronotum is greater than one-third (about 0.4) the width of the pronotum (state 2). In *K. taiwanensis* and *K. srilanka* the prepectus is much wider, greater than one-half (about 0.6) the width of the adjacent pronotum (state 1). My initial approach was to code a linear transformation series from the broad prepectus of *Perilampus* to the narrow prepectus of *Euperilampus* (Fig. 18a). This transformation was inconsistent with the final tree (CI = 0.75). This character was then analyzed as unordered allowing any possible transformation to add only a single step to the tree. This procedure resulted in a single shortest tree with this character exhibiting no homoplasy; the suggested transformation series is presented in Figure 18b. The cladogram (Fig. 19) suggests a revised interpretation of the evolution of the prepectus in the Perilampidae. The most parsimonious interpretation is that the common ancestor of *Krombeinius* and *Euperilampus* had a narrow prepectus (state 3), that a broader prepectus is a groundplan character in *Krombeinius* (state 2), and a still broader prepectus (state 4), approaching in size the prepectus of *Perilampus* (state 0), is a synapomorphy of *K. taiwanensis* + *K. srilanka.*

Character 3. The axillula is developed as a fingerlike lobe in all members of the *Perilampus hyalinus* group and in species related to *Perilampus platigaster* Say (Smulyan, 1936). A similar axillula occurs in *K. taiwanensis* (Fig. 6). The axillula is much shorter in all other species groups of *Perilampus* (state 0) and in related perilampid genera and the fingerlike configuration is therefore regarded as derived (state 1). The PAUP parsimony program suggests that the common ancestor of *Euperilampus* + *Krombeinius* and the *Perilampus hyalinus* group had the fingerlike axillula and a reversal occurred in the common ancestor of *Euperilampus* + *Krombeinius.* An equally parsimonious interpretation has the derived state occurring independently in the *P. hyalinus* group and in *Krombeinius taiwanensis.* I favour the latter interpretation and this example indicates the uncertainty that can be caused by apomorphies in the outgroup.

Characters 4, 5, 6. Three characters were used to describe the transformation series for the labrum. The labrum of all species of *Perilampus* shares the same basic configuration (Domenichini, 1969, Pl III, figs. 4, 5; Darling, 1987). Distinct aboral setae are present and the labrum does not have a deep median excision; there is no central stalk (states 0, 0, 0). Three derived characters are present in *Krombeinius* and/or *Euperilampus*: aboral digits reduced, setae sessile (states 1, 0, 0; Fig. 4); labrum bilaterally symmetrical, with deep median excision (states 0, 1, 0; Darling, 1983b,
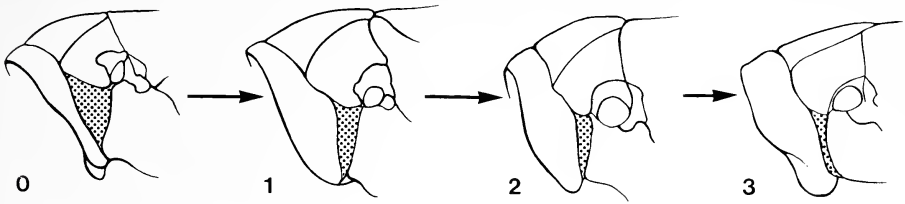
a) Ordered
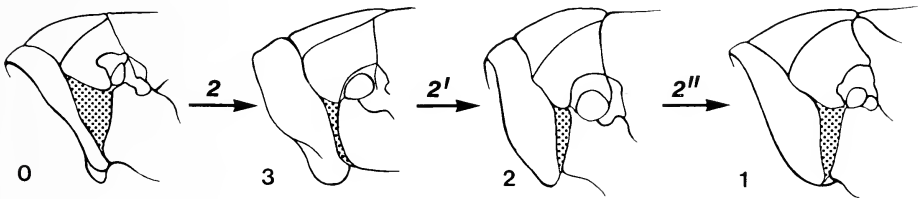
b) Unordered

Fig. 18.   Character states and possible transformation series for prepectus size (stippled), relative to width of adjacent pronotum (see "Phylogenetic Analysis," Character 2 in text).

fig. 3); labrum with a narrow central stalk, expanded distally with 7 or 8 short digits (states 0, 0, 1; Fig. 4).

Characters 7, 8. The third metasomal tergite is subequal in size to T2 in all species of *Perilampus* (states 0, 0). Specialization is judged to have resulted in two independent apomorphic states: T3 transverse, wider than long, much shorter than T2 along midline (states 0, 1; Darling, 1983b, frontispiece); T3 massive, as long as wide, longer than T2 along midline (states 1, 0; Darling, 1983b, fig. 1).

Character 9. As noted by Bouček (1978), the scutellum of *K. megalaspis* (fig. 2) is strongly convex in lateral view (state 1), a character shared with *K. taiwanensis* (Fig. 6). The scutellum is not strongly convex in lateral view, and tapers gradually towards the apex (state 0) in the outgroup, in *Euperilampus* and in all other species of *Krombeinius* (Fig. 13; Bouček, 1978, fig. 1; Darling, 1983a, fig. 1).

Character 10. The stigmal vein makes a 90° angle with the marginal vein (state 1) in *Krombeinius eumenidarum* and *K. saunion* (Darling, 1983a, fig. 1). The plesiomorphic state is an oblique angle (state 0) and is found in the outgroup, in *Euperilampus,* and in two species of *Krombeinius* (Rasplus, 1987, fig. 3). In *K. taiwanensis* the stigmal vein is coded as plesiomorphic, although the angle is somewhat intermediate (Fig. 8).

Character 11. In *Krombeinius eumenidarum* and *K. saunion* the lateral pronotum has a distinct callus suggesting bumpy shoulders (state 2; Bouček, 1978, fig. 1; Darling, 1983a, fig. 1). In the outgroup, *Euperilampus, K. megalaspis* (Bouček, 1978, fig. 2)

and *K. srilanka* (Fig. 13) the pronotum is regularly convex (state 0). A morphologically intermediate condition occurs in *K. lerouxi* and *K. taiwanensis*; the lateral pronotum is convex with only a slight indication of a callus (state 1; Fig. 6).

Character 12. The prepectus of Perilampidae is foveate, with many foveae occurring in *Perilampus* (state 0; Darling, 1983b, figs. 60, 61). In *Euperilampus scutellatus* and *Krombeinius megalaspis* there is only a single dorsal fovea (state 1). Multiple foveae are found in all other species of *Krombeinius* (Fig. 7; see also Bouček, 1978, fig. 1; Darling, 1983a, fig. 1). Although this character may be influenced by the absolute width of the prepectus (character 2), single and multiple foveae occur in species with the same configuration of the prepectus.

Character 13. The propodeum is very short in *K. megalaspis*, subequal in length to the metanotum (state 1). In *Perilampus* and all other species of *Euperilampus* and *Krombeinius* the propodeum is about twice as long as the metanotum (state 0).

Character 14. Smooth areas with reduced sculpture or completely devoid of sculpture (state 0) are usually present along the notauli in the Perilampidae and are present in the *P. hyalinus* group (Darling, 1983b, fig. 60). The mesoscutum is evenly sculptured only in the *Euperilampus scutellatus* and *E. tanyglossa* species groups, and in *Krombeinius megalaspis* (state 1).

Character 15. The inner orbits are developed as massive scrobal walls in all species of *Euperilampus* (Darling, 1983b, figs. 4–9) and to a lesser degree in the *Perilampus hyalinus* group (e.g., *P. carolinensis* and *P. regalis*). The inner orbits are not so developed in the plesiomorphic species groups of *Perilampus* and in related genera (*Burksilampus, Steffanolampus*). The massive scrobes are therefore regarded as plesiomorphic (state 0) in *Euperilampus* and *Krombeinius.* Only *Krombeinius taiwanensis* has reduced scrobal walls (state 1), here regarded as a reversal to the plesiomorphic condition.

Characters 16, 17. Two characters were coded to represent the sculpture patterns found in the various species. The third metasomal tergite is completely smooth (states 0, 0) in the *P. hyalinus* group. Distinct, but small, punctures are present laterad, near the border of T2 and T3 in two species of *Krombeinius* (states 1, 0). This sclerite is almost completely sculptured in *K. srilanka* (states 0, 1).

Character 18. Distinct tentorial pits (state 1) are present in *K. saunion* (Darling, 1983a, fig. 16). In all other taxa the tentorial pits are indistinct (state 0, Fig. 1; Darling, 1983a, figs. 8, 12; Darling, 1983b, figs. 5, 10, 11, 38). [Note: weak tentorial pits are present in *Euperilampus aureicornis* but not in its sister species *E. tanyglossa*.]

Character 19. The propodeum has a distinct median ridge in the *Perilampus hyalinus* group (state 0; Darling, 1983b, fig. 63). In *Krombeinius eumenidarum* and in all species of *Euperilampus* the median area of the propodeum is foveate and lacks a complete median ridge (state 1; Darling, 1983b, figs. 17–20). My previous cladogram regarded the lack of a median ridge as a synapomorphy of *Krombeinius + Euperilampus* (character 14); only the type species, *K. eumenidarum* was included as an exemplar. This character exhibits considerable homoplasy and is here interpreted as a synapomorphy of *Euperilampus* and also as a convergent autapomorphy of both *Krombeinius eumenidarum* and *K. srilanka.*

Character 20. The scutellum is developed as an elongate spine (state 1) in *K. saunion* (Darling, 1983a, fig. 15). The scutellum is truncate (state 0) in all other species of *Krombeinius* (as in Figs. 5, 12), in all species of *Perilampus,* and in *Euperilampus*

scutellatus. However, two species of *Euperilampus* (*E. gloriosus* and *E. spina*) have the scutellum produced as a prominent spine. These species are representatives of distinct species groups of *Euperilampus* (Darling, 1983b) and the spine-like scutella are also interpreted as non-homologous autapomorphies in these species.

Characters 21, 22. The relative length of the marginal vein is coded as two trans-formation series. The plesiomorphic state, found in *Perilampus hyalinus,* has the marginal vein longer than the postmarginal vein, but less than 1.5 times the length of the postmarginal vein (states 0, 0; Darling, 1983b, fig. 62). The marginal vein is very short in all species of *Euperilampus,* shorter than the postmarginal vein (states 1, 0; Bouček, 1978, fig. 6; Darling, 1983b, figs. 57–59). The marginal vein is slightly longer in most species of *Krombeinius,* marginal vein is between 1.5 and 2 times the length of the postmarginal vein (states 0, 1; Fig. 8; Darling, 1983a, fig. 1). The only exception is *K. srilanka* in which the marginal vein is only 1.35 the length of the postmarginal vein; here regarded as a reversal to the ancestral condition. Character 21 is an unequivocal synapomorphy for *Euperilampus.* However, character 22 is somewhat less certain. Homoplasy is present and the observed differences are subtle. This hypothesis will have to be tested when the species groups of *Perilampus* are considered in detail. In the final analysis both *Krombeinius* and *Perilampus* may be shown to have the plesiomorphic configuration of the marginal vein, an interpretation that would not affect the hypotheses of relationships (Fig. 19).

Character 23. The scutellum of all species of *Euperilampus* has a distinct crenulate marginal rim that is separated from the rest of the scutellum by a distinct carina (state 1; noted by Bouček, 1978, figs. 3–5, 7–11; Darling, 1983b, figs. 12–16, 34, 36, 37). The marginal rim is absent (state 0) in all species of *Perilampus* (Darling, 1983b, figs. 60, 61, 63, 66) and in *Krombeinius* (Fig. 5; Bouček, 1978, figs. 1, 2; Darling, 1983a, figs. 1, 7, 11, 15). The vaulted scutellum of *K. megalaspis* and *K. taiwanensis* (character 10) could be considered as a possible morphological intermediate to the marginal rim of *Euperilampus.* All that would be necessary is to delimit the apex of the scutellum with a complete carina. This, however, does not appear to be the case. If characters 10 and 23 are coded as a single linear transformation series with the vaulted scutellum as intermediate, additional steps would be added to the final cladogram. In addition, the scutellum of *K. srilanka* is most similar to species of *Euperilampus* (see description for details), and this species does not have a vaulted scutellum (Fig. 13).

Discussion. Figure 19 is the most parsimonious cladogram for the 23 characters (length = 36, consistency index with autapomorphies removed = 0.667); there are no other equally parsimonious trees. Trees slightly longer than the shortest possible tree were also evaluated for topology, in particular, monophyly of the recognized genera. There are 13 trees with length 37 of which 11 support monophyly of the genera. The strict consensus tree for these 14 trees is almost completely unresolved, only supporting the monophyly of the ingroup and the sister group relationship of *K. eumenidarum* + *K. saunion.* As discussed above, character 10 is somewhat tenu-ous. When this character is deleted there are 20 equally parsimonious trees (length = 35) and the consensus tree only recognizes the monophyly of *Euperilampus* + *Krombeinius.* The cladistic relationships for the species of *Krombeinius* are not robust and would be expected to change if additional taxa or characters were added to the analysis. In fact, two of the species were incorporated into the study after initial
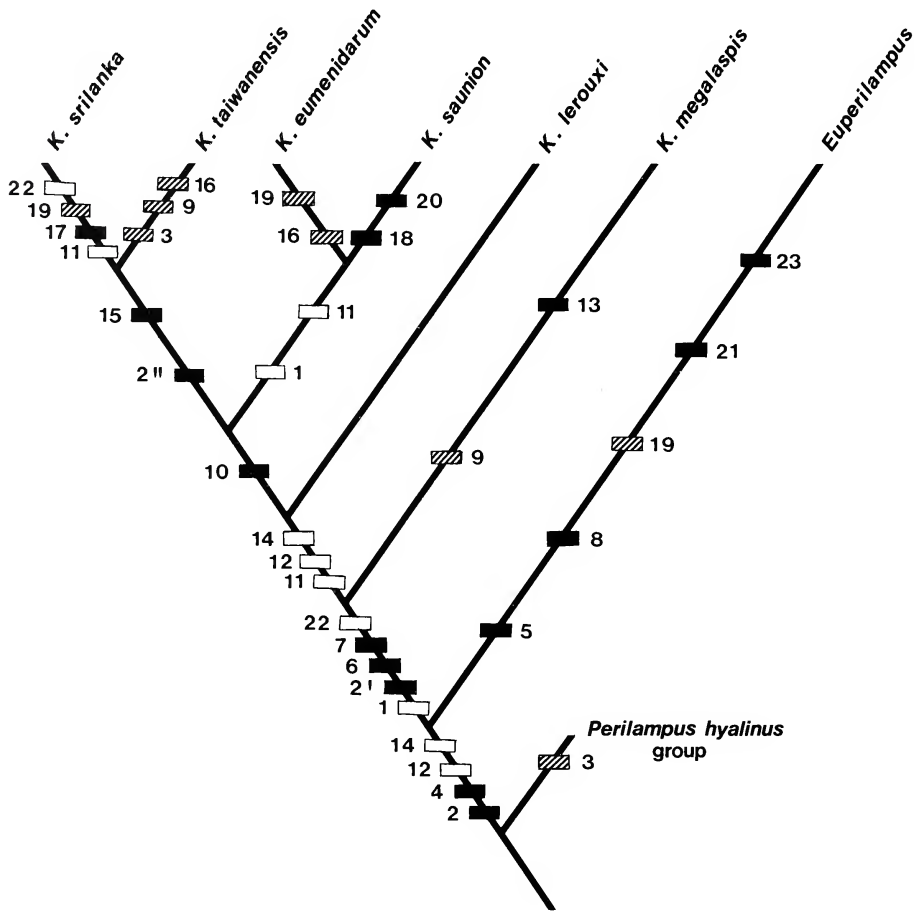
Fig. 19. Most parsimonious cladogram for data matrix in Table 1 (see text for discussion of character polarity and coding). Numbers refer to characters discussed in text and solid bars (■) indicate unique and unreversed apomorphies, and dashed bars (▨) indicate convergent apomorphies and open bars (□) indicate characters with reversals. The subsequent transformations of character 2 are indicated as 2' and 2".

analyses were completed (*K. lerouxi* and *K. srilanka*) and this did result in altered degrees of relationships.

A persistent source of confusion in cladistic analysis is the treatment of multistate characters. The use of the unordered algorithm of the PAUP program to interpret the evolution of pronotum shape suggests that considerable care should be exercised in the coding of multistate characters. The effect of coding transformation series as single linear sequences should be evaluated by comparison with alternative codings or by unordering the states. In many data sets homoplasy introduced by coding single intuitive transformation series results in multiple equally parsimonious trees which differ in topology. This problem is much more prevalent in data sets with low consistency indices. If classifications and binominal nomenclature are to be inex-

orably tied to cladistic analyses then considerable attention should be given to the assessment of not only equally parsimonious trees but also to slightly longer trees. Care should also be used in coding multistate characters.

In summary, the monophyly of *Krombeinius* is strongly supported by this analysis, as is the monophyly of *Euperilampus* and the sister group relationship of these genera. This analysis is also satisfying in that characters that should intuitively have a high weight, in particular complex, unique and unreversed morphological features (e.g., characters 2, 4, 6, 7, 8), support the major branch points, and characters that would be judged a priori to be evolutionarily labile, such as surface sculpture (e.g., characters 14, 16, 17) are interpreted as convergent similarities of terminal taxa.

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FURTHER STUDIES OF ASIAN MACROCERINAE (DIPTERA: MYCETOPHILIDAE), WITH THE DESCRIPTION OF A NEW CHIASMONEURINE GENUS, *LANEOCERA*

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Abstract.—*Laneocera,* a new Chiasmoneurine genus with a single included species, *L. magnifica* from southern India, is described. Four new species of *Macrocera, M. districta, M. alacra, M. elegantula* and *M. lacustrina* from the northern Indian subcontinent are described. Further records are furnished for *M. brunnea, M. inconspicua, M. nepalensis* and *M. simbhanjangana.* Wing photographs and drawings of mouthparts and terminalia are presented.

In 1913, de Meijere described the monotypic genus *Chiasmoneura* from Java with the unique female type, *C. anthracina.* In 1929, Edwards described a unique female, *C. cyclophora,* from the New Hebrides. Matile (1972) described four more species from the Ethiopian Region and also described a new genus *Chiasmoneurella* from that region. The new genus was based on differences from *Chiasmoneura* by antennal length and setation, and by development of the wing veins. In a collection of fungus gnats taken by F. Schmid in southern India, I have two specimens of a closely related form which I am referring to a new genus based on differences of female abdominal structures, the lack of a projecting vertexal prominence, the degree of development of the clypeus and the development of the wing venation.

The last study of Asian *Macrocera* was that by Coher (1963). The Asian material in the present study, mostly collected by F. Schmid, adds four new species from the northern portion of the Indian subcontinent. New data are given for four species: *M. brunnea* Brunetti, 1912; *M. inconspicua* Brunetti, 1912; *M. nepalensis* Coher, 1963 and *M. simbhanjangana* Coher, 1963. A complicated macrocerine fauna has developed in Southeast Asia, showing a connection to the African fauna as principally illustrated by the Chiasmoneurini.

Holotypes are deposited with the National Museum of Natural History, Washington, D.C.

Laneocera, new genus

Diagnosis. This south Indian macrocerine genus related to *Chiasmoneura* is unique in several respects and broadens the characterization of the Chiasmoneurini. The genus, which is described from female specimens only, is principally characterized by reduced venation at fM, genital flaps on SVII and a reduced vertexal area.

Description. Female. 4.5 mm. Head with vertexal area not protruding, three equal ocelli, laterals on small prominences separated by a wide furrow with the median ocellus anterior; eyes ellipsoid; antenna filiform and at least as long as body; clypeus (Pl. 1) strongly inflated, setose; mouthparts (Pl. 1) strongly developed and curved

around and appressed to ventral portion of the head. Thorax with pleura and scutellum bare; mesoepimeron very narrow ventrally. Wing (Pls. 1, 2), macrocerine, R3 absent; anterior branch of R not thickened where it meets the costa; base of M and fM nearly obsolescent; base of first branch of Cu obsolescent; anal veins strongly developed; long macrotrichiae over entire wing with costa strongly setose, apical and posterior margins finely setose. Abdomen with SVII modified so that a pair of genital flaps (Pl. 1) is present; post-VII segments strongly reduced.

Male unknown.

Discussion. Chiasmoneurine elements of this genus are its habitus; the form of the head capsule; the long antennae; the setiferous, inflated clypeus; the mouthparts large and produced beneath the head; the proportions and form of the pleural sclerites; the pattern, venation, setation and form of the wing; the strongly reduced terminal abdominal segments. This macrocerine fly closely resembles a *Chiasmoneura,* but, the reduced vertexal area, the presence of genital flaps and reduced venation at fM are unique and serve to easily separate the two genera.

Type species. Laneocera magnifica n. sp. described as follows.

Laneocera magnifica, new species

Diagnosis. Not presently closely related to any other Chiasmoneurini but clearly a member of that taxon.

Description. Female. 4.5 mm. Head brown, vertexal area subpentagonal, not produced and bare; occipital area lighter brown with strong brownish setae; eyes ellipsoid; lateral ocelli their own diameter from eye margin, each situated on a low prominence and separated by a broad median furrow with an anterior ocellus; antenna filiform with scape inflated and setiferous, pedicel doughnut-shaped, flagellar segments one to nine subequal in length; scape, pedicel and first flagellar segment yellowish brown, segments two to five with a narrow basal and distal yellowish band, remainder brown except for missing distal segments, flagellum at least as long as body; clypeus strongly inflated, setose (Pl. 1); palpi brown, four-segmented plus a basal boss, second, third and fourth segments flattened, second segment broadened apically with the third segment arising pre-apically from it; mouthparts well-developed, lying below the ventral surface of the head and strongly appressed to it. Thorax shiny red-brown, mesonotal setae sparse and short, humeri narrowly yellow-brown; pleura bare, mesoepimeron reduced so that it is very narrow ventrally, katepisternite about twice as large as anepisternite, anterior pronotum yellow-brown, scutellum and pronotum bare. Legs with forecoxa yellowish, mid coxa and hind coxa distally yellow-brown; femora yellowish basally, light brown distally, all legs appearing darker apically; hind femur narrow at base and widening apically; foretibia inflated apically; tibiae with apical with apical spurs subequal to terminal width of tibiae. Wing (Pls. 1, 2) with macrotrichia which are reduced in area of anastamosis; R3 absent; costa very setose. Halter yellow-brown with a long stem. Abdomen shiny red-brown, TI laterally yellow-brown, TV and TVI lighter, SIII also appearing lighter anteriorly. SVII divided into a pair of flaps (Pl. 1); segment VIII strongly reduced. *Note:* the posterior portion of the holotype abdomen was lost after the preliminary pencil sketches were completed. The illustration is from that sketch and represents the appearance as best as can be presently demonstrated.

Male. Unknown.

Holotype. INDIA: Madras, Devala, 3,000', 8 January 1959.

Paratopotype. Same data, abdomen incomplete, sex unknown. In my personal collection.

Macrocera brunnea Brunetti, 1912

Male. Wing with R5 at most one half as long as M1 + 2. Dististyle of the Singtam specimen narrower towards its base than that of the typical form.

Records. INDIA: West Bengal, Singtam, 2,625', 11 March 1959, male; Madras, Ootacamunda, 7,200', 25 December 1958, 3 males.

Discussion. The known range of *brunnea* is extended about 1,000 miles southward from south of Himalayas to a higher altitude in southern India. The discontinuous range is probably due to lack of collecting records from intermediate areas.

Macrocera nepalensis Coher, 1963

Male. Abdomen with TI yellowish, TII–TIV with narrow anterior dark band, TV–TVI chestnut. Wing with Sc sparsely setose; length of R4 half of M1 + 2. Rumkheng male with R4 subequal to M12, tip of M1 bent towards R5, dististyle of terminalia subrectangular (possibly an artifact of a unique, uncharacteristically hardened specimen even after maceration in potassium hydroxide).

Female. Unknown.

Records. INDIA: Agra, 4,000', 5 April 1958; Assam, Shnongpdeng, 1,000', 7 April 1960; Rumkheng, 3,000', 20 March 1960; West Bengal, Singtam, 2,625', 11 March 1959, 2 specimens; Kumaon, Dobalgaon, 5,000', 14 April 1958.

Discussion. It is of interest to note the prehensile tarsi of this species which suggests a habit of hanging on spider webs or fungal mycelia, or perhaps a use in mating. The specimen from Rumkheng is double the size of all other known specimens.

Macrocera inconspicua Brunetti, 1912

Male. 5.5 mm. Antenna 5× body; mesonotum with median anterior chestnut stripe about ⅔ its length and with two lateral stripes from posterior margin to anterior fourth. Wing with C produced beyond apex of R5 about one-fourth of distal margin of cell R5. Abdomen with posterior margin of TII–TVII light.

Female. 5.5 mm. As for the male with a slightly more robust body. Wing with C only slightly produced beyond R5; tip of wing slightly more rounded than that of male. Setation of Cu1 and Cu2 heavier than that of male. Abdomen with posterior margin of all segments light.

Records. INDIA: Kumaon, Tarsali, 6,000', 6 May 1958, male; Binaik Chatti, 7,000', 16 June 1958, female.

Discussion. Although the color and pattern of the abdomens of both male and female do not match *inconspicua* as given by Brunetti, this is probably the species he had before him. The female is described for the first time. The male terminalia (Pl. 1) are figured for the first time. Based on the form of the dististyle it forms a complex with plain-winged Palearctic *M. crassicornis* Winnertz, 1863 and the pattern-winged Oriental species, *nepalensis* Coher, and *lacustrina* and *alacra* n. spp.
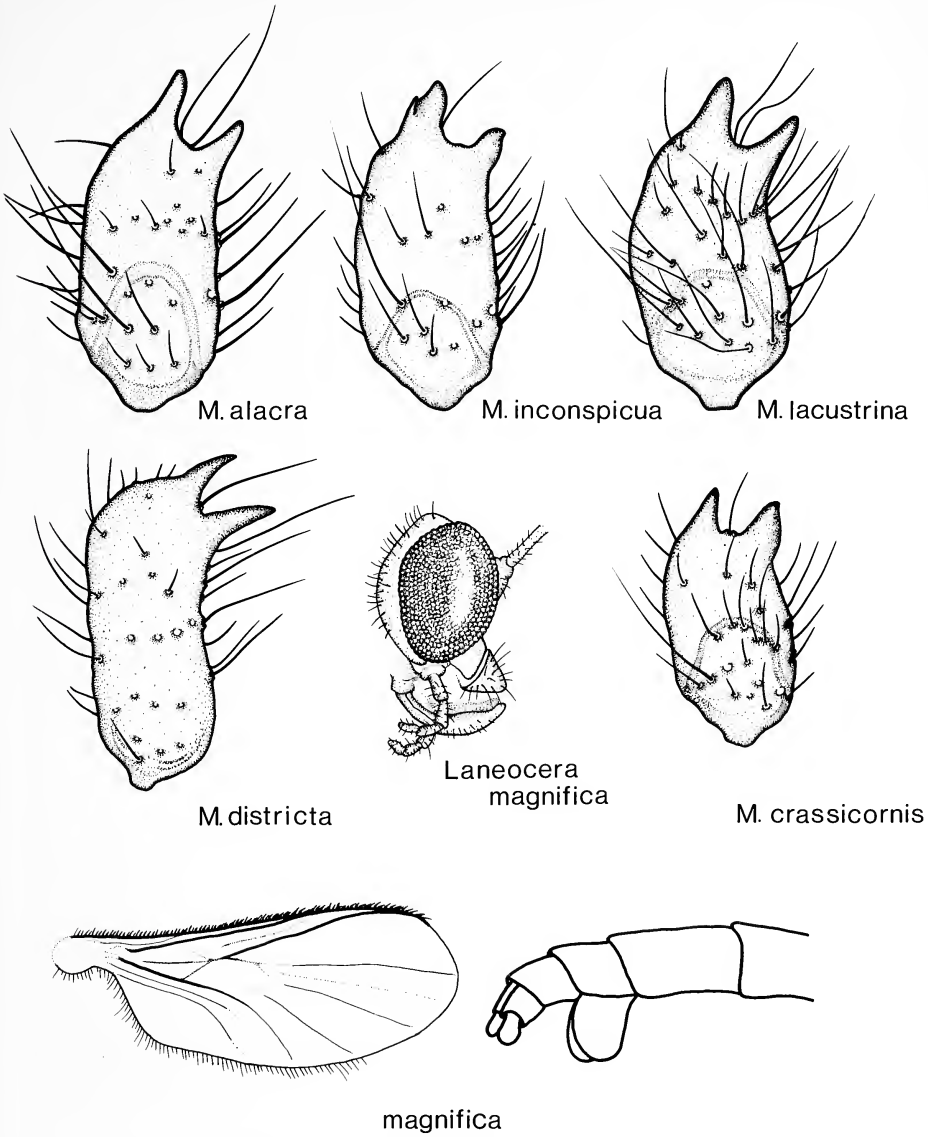
Fig. 1.   Dististyles of Asian *Macrocera* spp. with smaller setae omitted. Lateral view of head of *Laneocera magnifica*. Wing of *L. magnifica* to show venation, pigmentation omitted. Sketch of the terminal abdominal segments of the female types of *L. magnifica* showing genital flaps on segment seven. Not drawn to scale.

Macrocera simbhanjangana Coher, 1963

Records. NEPAL: Simbhanjang, 8,190', 1 October 1956, female; 19 October 1957, 2 males; 8,150', 17 April 1957, female; 24 July 1956, 2 males.

Discussion. Flies taken at 8,190' are topotypes.

Macrocera districta, new species

Diagnosis. This species is somewhat like *M. alacra* n. sp. in that both have a well developed subapical wing band. They are easily separated by other characteristics of the wing such as the heavy basal infuscation of *alacra* and the heavy apical infuscation of *districta* and its broad, subapical band which reaches to the posterior margin.

Description. Male. Head reddish brown; antenna 2× wing, with first four flagellar segments yellowish, remainder brown. Thorax with mesonotum red-brown, posterior margin of katepisternite yellow, scutellum yellow, postnotum mostly yellowish with some posteromedian red-brown. Wing (Pl. 2). Halter yellow. Legs yellow; forefemur 0.5 length of hind femur; forebasitarsus 0.9 length of foretibia, tarsi not prehensile. Abdomen with TI–TVI dark posteriorly, TII shorter than TIII and TIV and about half dark. Terminalia (Pl. 1) with dististyle subrectangular and with two terminal spines almost lateral.

Female. Unknown.

Holotype. IRAN: Waliabad, 16 September 1956.

Discussion. *M. districta* is the first Asian *Macrocera* to be described with a wing band which lies distad of the anastomosed veins and the fM1 + 2; the band runs from the point where both R1 and R4 join the costa, to the apex of Cu2 at the posterior margin of the wing. In addition, the wing tip is broadly infuscated. The terminalia are somewhat like those of *M. elegans* Brunetti, although the apical spines are shorter and more blunt and the base of the dististyle is broader and more rounded.

Macrocera alacra, new species

Diagnosis. This new species has, as its closest relatives, *nepalensis* and *districta*. It is easily separated from these by the much more highly infuscated area at the base of the anastomosis of M and Rs as well as having the wing band pass distad of the fM1 + 2.

Description. Male. 5–6 mm. Head brown to red-brown; palpus brown to red-brown; antenna 2–2.5× wing, yellowish. Thorax with mesonotum yellow-brown to reddish-brown with pale acrostichal stripes and a very narrow median pale stripe in the darker forms; pleura yellow-brown to red-brown; scutellum yellow-brown; postnotum yellow-brown to red-brown. Wing (Pl. 2), fR entirely infuscated or with proximal angle hyaline; apex with slight infuscation in cell R5 and M1 (Gangrea) or beyond Cu1 (Dobalbeta). Legs with forefemur about 0.5 length of hind femur and slightly shorter than foretibia; all tarsi prehensile. Halter with knob dark, stem pale. Abdomen brown with lateral pale area or entirely red-brown. Terminalia (Pl. 1) with a subrectangular dististyle with two simple terminal spines; apical spines of dististyle more robust in Gangrea material.

Female. 4.5–5 mm. With the same characteristics as the male except for antenna 1.5× wing length, more extensive darkening of the apex of the wing, forebasitarsus about 0.85 length of foretibia.

Holotype. Male. INDIA: Kumaon, Gangrea, 9,000', 12 June 1958.

Paratopotypes. Two males with the same data.

Paratypes. Male. INDIA: Kumaon, Trijugi Narain, 7,000', 26 May 1958; two females, Dobalbeta, 8,000', 30 May 1958.

Allotype. Same data as the holotype.

Discussion. This species has a wing band lying distad of the anastomosed veins and fM1+2. The band does not attain the posterior margin of the wing but nearly reaches Cu1 or extends just beyond it; the apex of the wing is variably infuscated. Despite minor differences in the Gangrea specimens, they are considered to be conspecific with the other material of *alacra*. Much more material will have to be examined to determine whether this approach is correct.

Macrocera elegantula, new species

Diagnosis. Presently, this species is considered to be separable from its nearest relative, *M. flavicosta* Brunetti, by its much more extensively trichiate wing membrane and darker markings of the wing along the coastal margin.

Description. Female. 6.5 mm. Head mostly red-brown, darker around ocelli; palpus red-brown; antenna at least 2× wing length, with scape and pedicel light brown, flagellum dark. Thorax with anepisternite, katepisternite and pleurotergite dark red-brown, mesoepimeron yellow-brown; mesonotum with light humeral area connected to light acrostichal stripes, remainder dark red-brown; scutellum yellow-brown; postnotum red-brown mediad, yellow-brown laterally. Forefemur less than half as long as hind femur. Forebasitarsus about 0.9 of foretibia. Wing (Pl. 2) with extensive macrotrichia apically in cell Sc and in all of cell R1+2+3, heaviest apically in cells R4, R5 and M1; M2 with trichiation occurring in a line to base, cells Cu1 and Cu2 with a similar line of setae less developed, anal cell with trichiation apically. Abdomen brown with light posterolateral areas on TII–TV; posterior segments damaged.

Male. Unknown.

Holotype. INDIA: Kumaon, Hanuman Chatti, 9,000', 30 June 1958.

Discussion. This species is closely related to or perhaps even conspecific with *flavicosta* but has more extensive markings along the costal area of the wing and a lighter but more extensive darkening around the apex of the wing than figured by Brunetti. The presence of extensive macrotrichia on the wing of this new species apparently serves to separate the two. *M. elegantula* has the most heavily trichiated wing of any Asian *Macrocera* known at this time.

Macrocera lacustrina, new species

Diagnosis. This species, which is close to *M. crassicornis* and *M. inconspicua,* can be separated from them by the infuscated marking at the anastomosis and fM of the wing. The wing is more yellowish than that of *crassicornis*; in *inconspicua,* the costa projects slightly beyond R1 and ends at the apex of the wing. The microtrichia of the wing are smaller than those on the membrane of *inconspicua* and the veins are less setose.

Description. Male. 5.5 mm. Head yellow-brown, antenna 1.5× wing length. Thorax yellow-brown, broad median stripe on anterior two-thirds with acrostichal stripes from posterior margin to humeral angle; pleura yellow-brown with lighter scutellum
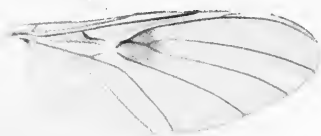
Fig. 2.   Wings of Asian *Macrocera* spp. and *Laneocera magnifica*. Not photographed to scale.

and postnotum. Legs with forebasitarsus 0.9 length of foretibia, foretarsi prehensile (other legs missing). Wing (Pl. 2), clear, with a small dark area at anastamosis and fM; C ends at apex of R1. Abdomen yellow with posterior third of T1–TVI red-brown. Terminalia (Pl. 1) with a subrectangular dististyle with two broad apical spines.

Female. Unknown.

Holotype. PAKISTAN: Kumaon, Hanuman Chatti, 9,000', 30 June 1958.

Discussion. M. lacustrina has been taken at a higher altitude than any other species of *Macrocera* known to me. The terminalia are rather similar to those of *alacra*. However, the terminal spines of *lacustrina* are distinctly broader as is the entire dististyle.

KEY TO *MACROCERA* BASED ON KNOWN MALES

The wing of *vishnui* is known only from a single damaged specimen; it appears to fit the second couplet of 1 in the following key. The terminalia of *alternata* have not yet been studied nor figured.

1. Wing infuscation primarily confined to the costal area above R5 and through the anastamosis 2
 – Wing unmarked or marked otherwise 3
2. Costal margin of wing with a series of five dark infuscated spots and with suffused areas between them . . . . *alternata*
 – Costal margin of wing with a single infuscated spot where R1+2+3 joins the costa and cell R4 infuscated except at base, very lightly suffused at apex of cell R5 and M1 . . . . *brunnea*
3. Wing plain, no infuscated pattern 4
 – Wing variously infuscated 5
4. Apex of wing suffused or hyaline; dististyle with a single large apical spine plus a small spine at its base . . . . *simbhanjangana*
 – Wing slightly suffused; dististyle with two broad apical spines one of which has sinuous margins and the other notched and doubled . . . . *inconspicua*
5. Wing with a subapical infuscated band originating at or below apex of R4 and distad of fM 6
 – Wing otherwise marked 8
6. Infuscated area at fR small, nearly lining veins . . . . *districta*
 – Infuscated area at fR widespread 7
7. Subapical wing band very broad, dark markings through the anal-cubital area . . . *ornata*
 – Subapical wing band about 3 times as long as wide, no dark markings in anal-cubital area . . . . *alacra*
8. Male dististyle with three long apical spines . . . . *trispina*
 – Male dististyle with two apical spines 9
9. Dististyle about 3 times as long as wide, curved 10
 – Dististyle about 1½ times as long as wide, subrectangular 11
10. No infuscation along R . . . . *elegans*
 – Wide infuscation along and above Rs . . . . *vishnui*
11. Infuscation at M and fM . . . . *lacustrina*
 – Infuscation at M, fM and base of M4 and at apex of R1+2+3, cells R5, M1 and extreme apex of M2 suffused . . . . *nepalensis*

KEY TO *MACROCERA* BASED ON KNOWN FEMALES

1. Wing plain, without infuscated pattern 2
 – Wing variously infuscated 3
2. Apex of wing suffused with a clear lighter band basad, an infuscated spot at the apex of R1+2+3 . . . . *simbhanjangana*
 – Wing clear, slightly yellowish, immaculate . . . . *inconspicua*
3. Wing with a subapical infuscated band originating at or below apex of R4 and distad of fM 4

–   Wing otherwise marked   5
4. Subapical wing band very broad, dark markings through the anal-cubital area .... *ornata*
–   Subapical wing band about 3 times as long as wide, no dark markings in anal-cubital
    area .... *alacra*
5. Apex of wing infuscated or heavily suffused   6
–   Wing narrowly infuscated along costal margin   8
6. Dark apical area broadly margining wing to anal area .... *elegantula*
–   Dark apical area reaching little, if any, beyond M4   7
7. Apical infuscated area mainly confined to cell R5 and less so in apex of cells R4 and
    M1, no infuscation between wing base and infuscated area that passes through the
    anastamosis .... *elegans*
–   Heavily suffused broad, apical spot from cell R4 to or beyond M3, small species,
    Thailand .... *femina*
8. Wing with two infuscated spots along the costal area, unpigmented areas appearing
    between them .... *brunnea*
–   Wing with four or five infuscated spots along the costal area, lightly pigmented area
    between these   9
9. Wing with four spots along costal area, no small infuscated spot above middle of Rs
    and little suffused posterior to M4 .... *flavicosta*
–   Wing with five spots along costal area, a small infuscated spot above middle of Rs and
    infuscated at bend of M4 and Cu1 .... *alternata*

DEDICATION

This paper is dedicated to my old friend John Lane who helped to introduce me to the study of fungus gnats. The new genus *Laneocera* is named in his memory.

LITERATURE CITED

Coher, E. I. 1963. Asian *Macrocera* Meigen, 1803, with some remarks on the status of the genus and related genera. Bull. Brooklyn Entomol. Soc. 1:23–36, 2 Pls.
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THE OZOPHORINI OF THE WESTERN UNITED STATES AND BAJA CALIFORNIA (HEMIPTERA: LYGAEIDAE)

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Abstract.—Nine species of Ozophorini from the Western United States and Baja California are treated, with a key and distributional records presented. Two species, *Ozophora occidentalis* and *O. salsaverdeae* are described as new. The status of species in the *Ozophora picturata* species group is discussed in detail.

The genus *Ozophora* is a large, complex taxon. Ashlock and Slater (1982) list 36 species in the genus. There are many Neotropical species yet undescribed.

Most species and genera of Western Hemisphere Ozophorini are Neotropical. The species present in the United States for the most part represent a northern extension of elements of this fauna. Within the United States two essentially distinct faunas are present. The first is largely confined to Florida. Its species are conspecific with, or similar to, those found in the Caribbean and the eastern lowlands of Mexico and Central America. The second occurs in the southwestern United States from Texas and Kansas westward to the Pacific Coast. This fauna is similar to that found on the Mexican Plateau.

There is, however, one species complex which occurs primarily in the United States and extends southward only into northern Mexico. I call it the "*picturata*-group." The study was originally undertaken to attempt to understand the relationships of the components of this group.

However, included in the paper are all of the species of Ozophorini that are at present known to occur in the western United States. The fauna consists of seven species of *Ozophora* and one species of *Balboa*. Students should be able to identify all of the species of the tribe presently known to occur in the United States by using this paper and that of Slater and Baranowski (1984) which treats the Floridian fauna. A species as yet known only from Baja California is also included primarily to clarify its relationship to *Balboa ampliata* Barber.

All measurements in this paper are in millimeters.

KEY TO SPECIES OF OZOPHORINI OF THE
WESTERN UNITED STATES

2(1). Lateral margins of, at least, anterior pronotal lobe sharply acute, with a knife-like edge 2
–   Lateral margins of pronotum bluntly produced, edge obtusely ridged, "calloused," not sharply acute and knife-like 5
2(1). Dorsal coloration almost uniformly dark brown 3
–   Dorsal coloration pale yellow, or variegated 4

3(2). Lateral margins of corium with a distinct stridulitrum present; lateral margins of pronotum evenly convex .... *Balboa ampliata*
–   Lateral margins of corium with uneven surface but lacking a distinct stridulitrum; lateral margins of pronotum deeply, concavely sinuate .... *Ozophora unicolor*
4(2). Body coloration variegated, with a conspicuous pale macula present distally on each corium; humeral angles of pronotum "notched"; metathoracic scent gland auricle elongate, curving in an even arc to reach at least middle of metapleuron .... *Ozophora consanguinea*
–   Body uniformly bright yellow lacking any variegation of color and completely lacking a differentiated pale macula distally on corium; humeral pronotal angles evenly rounded; metathoracic scent gland auricle short, finger-like, not arcuately curving and not extending completely over inner ½ of metapleuron ...... *Ozophora angustata*
5(1). Very small species, considerably less than 5 mm in length; posterior meeting of bucculae U-shaped .... *Ozophora maculata*
–   Larger species, 6 mm or more in length; posterior meeting of bucculae V-shaped ..   6
6(5). Body very elongate and slender, length of body 16 or more times interocular distance .... *Ozophora depicturata*
–   Body relatively much shorter, length of body less than 14 times interocular distance   7
7(6). Posterior pronotal lobe with a narrow pale median streak running through dark central "ray"; apex of corium usually marked with crimson; fourth antennal segment with a large white basal annulus .... *Ozophora picturata*
–   Posterior pronotal lobe with median area completely dark brown; apex of corium lacking a crimson mark; fourth antennal segment with or without a white basal annulus   8
8(7). Fourth antennal segment uniformly or almost uniformly dark brown; mean length of fourth antennal segment more than 1.3 mm (Fig. 1) .... *Ozophora salsaverdeae*
–   Fourth antennal segment with a conspicuous pale basal annulus; mean length of fourth antennal segment less than 1.15 mm (Fig. 1) .... *Ozophora occidentalis*

THE *PICTURATA* GROUP

The taxonomic relationships of the members of this complex present a most interesting problem. I recognize three species, but suggest that additional study is needed to see if populations are reproductively isolated, or if intermediate populations occur.

Throughout the eastern United States (including part of Florida), west into northern Mexico and eastern Texas (northern limits in the west not well understood) occurs a rather homogeneous population recognizable by the possession of a broad white subbasal annulus on the fourth antennal segment, a crimson tinge at the apex of the corium, a complete broad dark brown strongly contrasting transverse fascia across the middle of the hemelytra, and a narrow pale streak in the middle of the dark median "ray" on the posterior pronotal lobe. This is the species described by Uhler as *picturata* from Massachusetts.

From eastern Kansas, southern and central Texas westward through Arizona, and into extreme southeastern California occurs a somewhat smaller population recognizable by its completely dark brown fourth antennal segment, lack of crimson coloration on the corial apex, completely dark brown median ray on the posterior pronotal lobe, and relatively pale brown hemelytron in which the transverse fascia is obscure and frequently interrupted laterally (Fig. 3). This is the species described below as *salsaverdeae*.
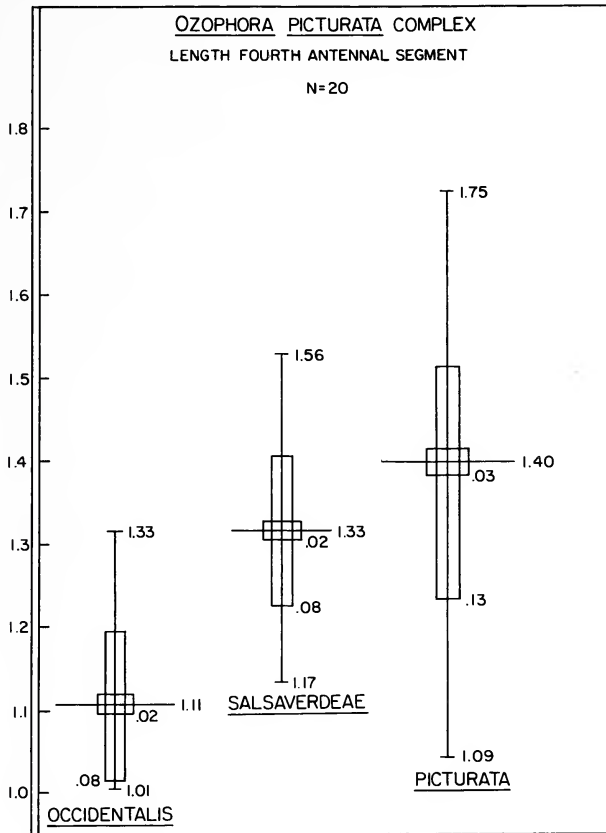
OZOPHORA PICTURATA COMPLEX

LENGTH FOURTH ANTENNAL SEGMENT

N=20

1.8

1.7 — 1.75

1.6

1.5 — 1.56

1.4 — 1.40 .03

1.3 — 1.33   .02 1.33   .13

1.2 — 1.33   .08

1.1 — .02 1.11   SALSAVERDEAE

1.0 — .08 1.01   1.17   1.09

OCCIDENTALIS   PICTURATA

Fig. 1.   Relative lengths of fourth antennal segment of *Ozophora picturata, O. salsaverdeae,* and *O. occidentalis.*

In California west of the desert and the Sierra Nevadas and extending northward into British Columbia occurs a population that resembles *salsaverdeae* in size and shape, in having a completely brown median posterior pronotal ray, in lacking a crimson corial apex, and in having an obscure reduced transverse hemelytral fascia. This population has a distinct white annulus on the fourth antennal segment. The fourth antennal segment is appreciably shorter than that of *picturata* (Figs. 1, 2). The white annulus is only one-half to one-fourth as long as that found in eastern *picturata.* This is the species described below as *occidentalis.*

The genital capsules and parameres of these populations show some differences, but are variable and do not seem to offer reliable differentiating characteristics.

The presence or absence and size of the white annulus on the fourth antennal segment is an almost constant feature, although occasionally in *salsaverdeae* there is an obscurely paler area near the base of the segment. The presence or absence of a pale streak mesally in the dark median ray on the posterior pronotal lobe is difficult
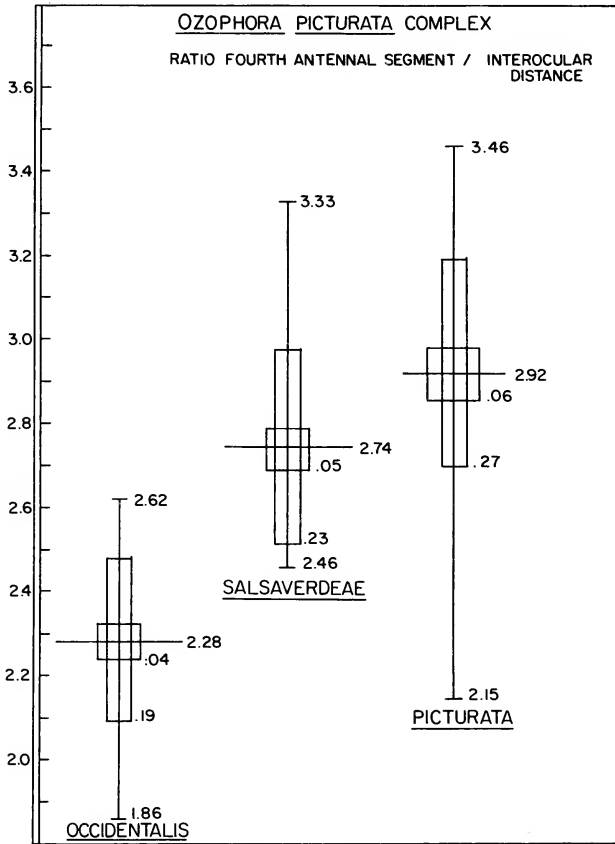
Fig. 2.   Ratio of length of fourth antennal segment to interocular distance of *O. picturata,*
O. salsaverdeae, and *O. occidentalis.*

to use in pale specimens where the rays themselves are obscure. The crimson mark
at the apex of the corium appears to fade (perhaps with age or with preservation in
alcohol). In any event it is not an absolutely constant feature. The transverse fascia
is variable and in some western specimens where the entire hemelytron is relatively
obscurely colored it is difficult to determine whether the fascia is complete or in-
complete. This is the most difficult "distinguishing" feature to use, and although
useful when one becomes familiar with the different taxa, it is difficult to define in
a meaningful way.

The essential problem is to determine what taxonomic status should be assigned
to populations of "*picturata*," "*salsaverdeae,*" and "*occidentalis.*" Although they are
for the most part allopatric, there are no constant genitalic differences and there is
overlap in the absolute length and relative length of the fourth antennal segment
(Figs. 1, 2). These facts suggest that they might well be considered as subspecies in
the traditional sense of the term. I believe the weight of evidence indicates that
recognition as distinct species is preferable for the following reasons. (1) In Texas

typical "eastern appearing" populations of *picturata* occur well west of typical specimens of *salsaverdeae*. (2) Typical eastern *picturata* individuals are known from northern Mexico whereas specimens from several localities in Texas along the eastern Rio Grande Valley (including Brownsville) are typical *salsaverdeae*. Thus "typical" *salsaverdeae* occurs geographically between the Mexican *picturata* population and the main range of *picturata*. (3) In the area around Brazos County, Texas both *picturata* and *salsaverdeae* occur without any evidence of intergradation. (4) A breeding population of *salsaverdeae* with no suggestion of *picturata* characteristics occurs in extreme eastern Kansas (Lawrence). This pattern scarcely suggests a subspecific taxon. (5) I have examined 4 specimens (3♂♂, 1♀) taken in the Huachuca Mountains ("Cochise Co., Upper Miller Cyn. 6,000–7,000', Huachuca Mts. 8.VIII.1974, J. Powell, under bear scats") that probably represent an isolated western population of *picturata*. That these specimens are all submacropterous makes comparison with other specimens of *picturata* difficult since the species has previously been known to exist only in the macropterous condition. These specimens have a noticeably reduced posterior pronotal lobe (a condition frequently associated with wing reduction) and the scutellum lacks the diagonal pale vittae that are usually present in *picturata*. The scutellum of these Miller Canyon specimens is paler on the posterior portion than it is anteriorly. In several specimens of *picturata* from Texas the pale vittae tend to coalesce to form a similar condition. It is also true that Texan and Mexican specimens of *picturata* tend to have a somewhat narrower pronotum than is generally true of specimens from eastern North America.

The fourth antennal segments of the Miller Canyon specimens have a large white basal annulus and both the segment and the white annulus are much more elongate than is true of *occidentalis*. In addition, the meson of the posterior pronotal lobe has a narrow pale streak which is characteristic of *picturata* and which is not found in either *salsaverdeae* or *occidentalis*.

These are particularly important specimens for two reasons. First, they establish the presence of *picturata*, at high elevations at least, far west of where it has previously been known, thus considerably strengthening my conclusion that *salsaverdeae* is a distinct species and not a geographic race. Second, these are the only specimens of the *picturata* complex that have reduced wings (which once again emphasizes the importance of collecting *in situ* and at high elevations).

I recognize the preliminary nature of this analysis. The samples do not represent a complete picture of the geographic range of these taxa. We do not have any information on genetic compatibility, and while we do know something of the biology of *picturata* we do not have any information other than brief habitat notes about *salsaverdeae* or *occidentalis*. The evidence at hand suggests that we are dealing with distinct species and they are so treated in this paper.

Ozophora picturata Uhler

Ozophora picturata Uhler, 1871:102–103.

Discussion. This species has much the same color pattern as described for *salsaverdeae* and *occidentalis* except that the pale and dark areas of the dorsal surface of the body are usually strongly contrasting. As noted in the key and general discussion,

picturata usually has a crimson corial apex and a pale median streak on the central dark ray of the posterior pronotal lobe.

The white annulus on the fourth antennal segment is always large, white, and in strong contrast to the dark distal portion of the segment.

This is the only ozophorine found over most of the eastern and central United States. Sweet (1964), who has studied its biology in Connecticut finds it to be the only seed feeding lygaeid living in the climax oak-hickory community of the northeastern United States. Its habits in the southern and western parts of its range are unknown. Slater and Baranowski (1984) describe the fourth and fifth instar nymphs.

Distribution. O. picturata is distributed throughout the eastern and central United States from Maine to Florida and westward to northern Mexico, Arizona, Texas, Oklahoma and Kansas. Slater (1964) lists it from Connecticut, Florida, Georgia, Illinois, Indiana, Iowa, Maryland, New Jersey, New York, North Carolina, Pennsylvania, South Carolina, Texas, Ontario and Mexico.

Material examined. From new areas in the United States and Mexico as follows: ALABAMA: Gulf Shores St. Pk., Flash Is., end Hwy 6 (Baldwin Co.). ARKANSAS: Magazine Mt. (Cameron Bluff). MAINE: Camden. MISSISSIPPI: Gulfport, 1 mi SE Ecru (Pontotoc Co.). Starkville. 6 mi SW Starkville. Adaton. nr. Craig Springs (Oktibbeha Co.). nr. Thaxton, Benson Farm, 3 mi WSW Sardis (Panola Co.). 2 mi N Waveland, Bayou la Croix (Hancock Co.). Monroe Co. Yalabusha Co. Ocean Springs. Gulf Is. Natl. Sea. [shore] (Jackson Co.). OHIO: Silver Lake (Logan Co.). Spencer Twp. (Lucas Co.). Lake Texoma (3 mi E Willis). TENNESSEE: Cumberland Co. VIRGINIA: Lake Drummond. Vienna. MEXICO: 15 & 16.5 mi W Linares (Nuevo Leon); Cacaheramilpa Cave (Guerrero).

Although *picturata* has been reported previously from Texas and Mexico (see Slater, 1964), some of these records probably were based upon other species. The following are definite *picturata* records: TEXAS: College Station (Brazos Co.). Bastrop. Sinton. Garner St. Park (Uvalde Co.). 3 mi E Old Dime Box (Burleson Co.). Navasota. Goose Island State Park (Aransas Co.). Palmetto State Park (Gonzales Co.). Dimit Co. Pt. Laraea, Chisos Mts. (Brewster Co.). Wilder Wildlife Refuge (San Patricio Co.). Harlingen (Val Verde Co.). Dolan Creek Camp Ground (Lee Co.). Giddings (Comanche Co.) nr. Proctor.

The records of *picturata* from Arizona by Snow (1904, 1906) are presumably referable to *salsaverdeae,* that of Johnson and Ledig (1918) to *occidentalis.*

The record of Gibson (1919) from Dominica and that of Gibson and Carrillo (1959) from Mexico cannot be placed without reexamination of specimens but certainly do not belong to *picturata.*

Ozophora salsaverdeae, new species
Fig. 3

Description. General coloration dull straw yellow. Head, anterior pronotal lobe and scutellum dark red brown. Posterior pronotal lobe with an obscure median and two sublateral dark brown longitudinal stripes or rays present; those midway between meson and lateral margins not reaching posterior margin of pronotum; median ray completely dark brown lacking a pale median streak. A pair of dull yellow divergent scutellar vittae present; extreme apex of scutellum white. Corium nearly uniformly pale brownish-yellow, but with obscure brown maculae as follows: large dark corial
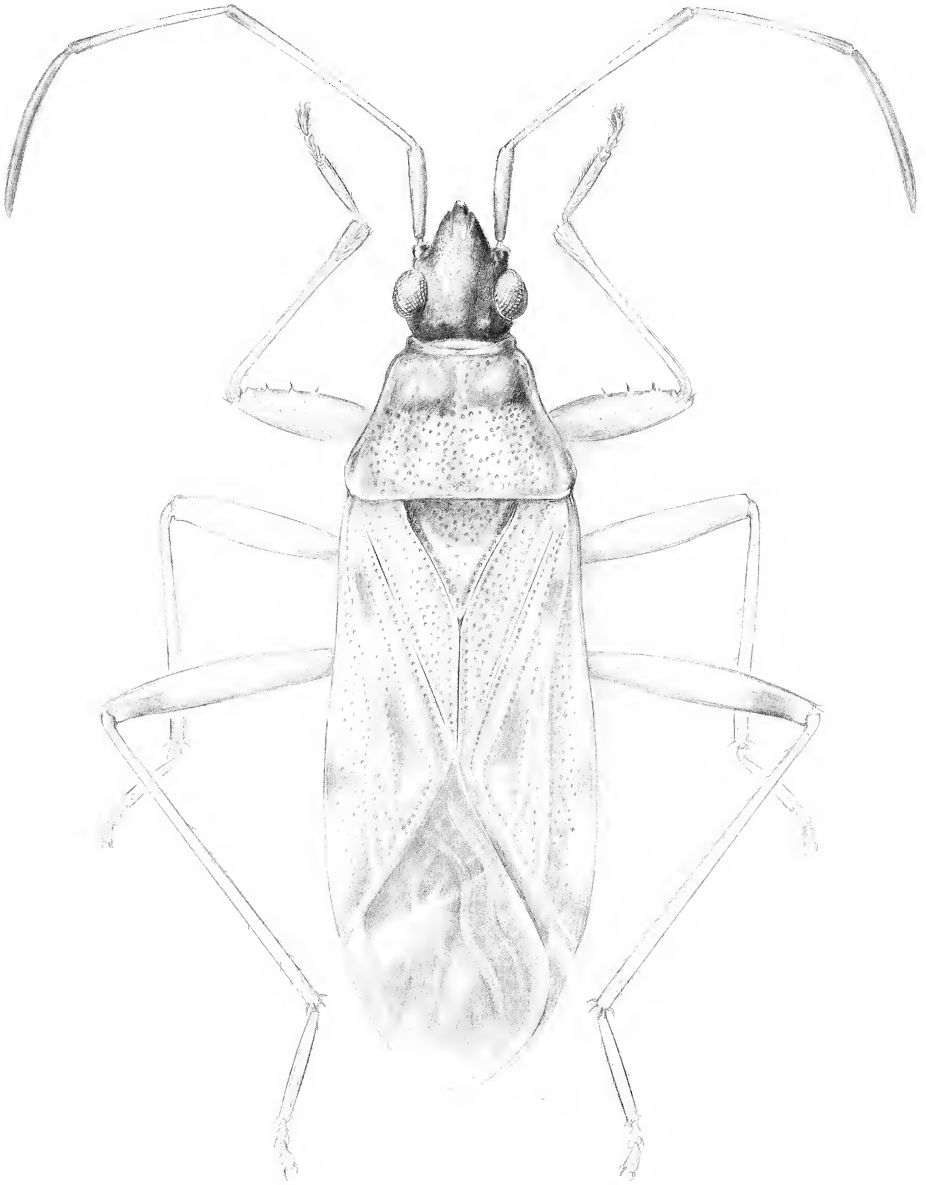
Fig. 3. *Ozophora salsaverdeae* new species. Dorsal view.

apex, a small rectangular patch along radial vein at level of apex of scutellum, a more or less complete but obscure transverse fascia, this including a dark macula on explanate marginal area that reaches lateral margin (these markings in areas similar to those of many species of *Ozophora* but extremely obscure in this species). Ap-

pendages largely pale yellow. Distal end of third antennal segment and all of segment four dark brown. Posterior femora with a weakly developed subdistal dark annulus. A few scattered, short, but upright hairs present on dorsal surface.

Head non-declivent; tylus at most attaining middle of first antennal segment; vertex moderately convex. Length head 1.0, width 0.96, interocular space 0.46. Pronotum with lateral margins sinuate; posterior margin straight; transverse impression complete but shallow mesally. Calli of anterior pronotal lobe impunctate, shining; areas laterad of calli pruinose. Length pronotum 1.02, width 1.58. Scutellum with pale laevigate oblique vittae confined to posterior half, coalescing at posterior ends. Length scutellum 0.88, width 0.80. Hemelytra gradually broadening posteriorly so that maximum width is at a level slightly caudad of posterior end of claval commissure. Length claval commissure 0.86. Midline distance apex clavus-apex corium 1.40. Midline distance apex corium-apex membrane 0.54. Metathoracic scent gland auricle elongate, slightly curving posteriorly. Fore femora armed below with three major spines. Labium reaching well between metacoxae, first segment reaching base of head. Length labial segments I 0.92, II 0.98, III 0.74, IV 0.42. Length antennal segments I 0.74, II 1.60, III 1.16, IV 1.40. Total body length 6.08.

Holotype. ♂, TEXAS: Jeff Davis Co., 1 mi W Ft. Davis, 15 August 1965 (at light) (J. C. Schaffner). In American Museum of Natural History.

Paratypes. ARIZONA: 2♀♀, Pepper Sauce Canyon, 15.VIII.1921, Santa Catalina Mts. (E. P. Van Duzee). 1♂, 1♀, Patagonia, Santa Cruz Co., 19.VI.1964 (uv light) (D. R. Smith & C. W. Baker). 1♂, Bradsh Mt., 21.VI.1942. 1♂, Patagonia, Santa Cruz Co., 27.VII.1956 (C. W. O'Brien). 3♂♂, 4♀♀, Patagonia, 3.VIII.1924 (E. P. Van Duzee). 2♂♂, 2♀♀, Pena Blanca Lk, 16 mi NW Nogales, Santa Cruz Co., 26.VII.1964 (uv light) (D. R. Smith & C. W. Baker). 2♂♂, 2♀♀, 14 mi E Oracle, 27.VII.1924 (E. P. Van Duzee). 2♂♂, 17♀♀, Oak Creek Canyon, 6 mi N of Sedona, 21.VII.1958 (at light) (C. W. O'Brien). 1♀, 10 mi N Sedona, Oak Creek Canyon, 20.VIII.1957 (C. W. O'Brien). 3♀♀, Noah Creek, Graham Mts. & Co., 4.VIII.1958 (light trap) (C. W. O'Brien). 1♂, same except 31.VII.1957. 3♂♂, Cochise Stronghold, Dragoon Mts., 29.VII.1957 (C. W. O'Brien). 1♀, same except 13.VIII.1958. 5♂♂, 4 ♀♀, Madera Canyon, Santa Cruz Co., 15.VII.1963 (V. L. Vesterby). 3♂♂, 2♀♀, Sabino Canyon, Santa Catalina Mts., 11.VII.1957 (at light) (C. W. O'Brien). 1♀, Prescott, 8.VII.1917 (C. A. Hill). 1♀, Washington Mts., nr. Nogales, 7.IX.1927 (J. A. Kusche). 1♂, Carr Canyon, Huachua Mts., 7.VII.1930 (J. O. Martin). 1♀, near Tucson, Pima Co., 8.VII.1957 (at light) (C. W. O'Brien). 1♀, Tucson, 15.III.1937 (Bryant) "13." 1♀, Santa Rita Mts., 5,000–8,000 ft, "VI" (F. H. Snow). 1♀, Rustler's Park, Chiricahua Mts., 6.VIII.1958 (R. E. Rico). 1♂, Cactus, 1.IX.1952 (N. T. Davis). 1♀, St. Xavier Mts., Tucson, 29.VII.1924 (J. O. Martin). 1♀, Santa Catalina Mts., 18.IV.1937 (Bryant). 3♂♂, 2♀♀, 10 mi E Apache, Peloncillo Mts., Cochise Co., 15.VIII.1972 (R. F. Denno, K. Yeargan, J. R. Bennedict). 1♂, 5 mi W Portal, 5,400 ft, Cave Creek Canyon, Chiricahua Mts., Cochise Co., 7.VII.1956 (M. Cazier). 1♀, same except 19.VII.1956. 1♀, same except 4.VIII.1956, (C. and M. Cazier). 1♀, same except 22.VI.1957, (M. Statham). 1♀, same except 4.VII.1957. 1♂, same except 1.VIII.1957. 1♀, same except 1.VII.1959. 1♀, same except 11.VII.1959. 1♀, same except 15.VII.1959. 1♀, same except 6.VII.1957 (Berlese trap) (C. W. O'Brien). 1♀, same except 10.VIII.1957. 1♀, same except 25.VI.1958 (M. A. Cazier). 1♂, same except 8.VIII.1958. 1♀, same except 22–23.VII.1960 (C. and M. Cazier). 1♂, same except (at light) 15.VII.1960 (J. M. Linsley). 1♂, same except

9.VIII.1961 (J. F. Lawrence). 1♀, same except 28.IV.1962 (J. A. Woods). 1♂, 1♀, same except 16.VII.1964 (W. J. Gertsch, J. A. Woods). 1♂, 1♀, same except 17.VII.1964 (J. A. Woods). 1♀, same except 14.VI.1965 (J. H. Davidson, J. M. Davidson, M. A. Cazier). 1♂, same except 20.VII.1970 (M. H. Muma). 6♂♂, 5♀♀, Molino Basin, Sta. Catalina Mts., Pima Co., 2.VIII.1970 (J. Powell, P. Rude). 1♂, 3♀♀, Stewart Camp 1 mi S Portal, Cochise Co., 18–20.VII.1971 (light trap) (J. T. Doyen). CALIFORNIA: 1♂, 2♀♀, Wild Rose Canyon, Death Valley National Monument, Inyo Co., 7.XI.1957 4,000 ft (*Neotoma* nest of wild rose and willow) (R. E. Ryckman, J. P. Fonseca). COLORADO: 1♀, Denver, 29.III.1963 (J. T. Polhemus). KANSAS: 1♂, Salina, SA Co., 9–14.IX.1973 (H. D. Engleman). 2♂♂, 1♀, Mead Co. St. Lake and Park, 25.VII.1978 (at light) (A. Slater, S. W. Hamilton). 1♀, Douglas Co., Lawrence, 21.VI.1970 (P. D. Ashlock). 1♀, same except 8.IX.1979 (A. Slater). 1♀, same except 23.IX.1979 (P. D. Ashlock). 1♂, 1♀, same except 24.VI.1980. 1♂, 2♀♀, same except 30.VI.1980. NEW MEXICO: 1♀, Big Dry Creek, Grant Co., 10.IX.1933 (H. S. Gentry). TEXAS: 1♀, Ft. Davis, 27–29.VIII.1962 (H. R. Burke). 1♂, 5♀♀, Ft. Davis, Limpia Canyon, 20.VI.1964 (M. H. Sweet). 9♂♂, 11♀♀, Jeff Davis Co., 1 mi W Ft. Davis (at light) 15.VIII.1965 (J. C. Schaffner). 1♂, same except 16.VIII.1965. 1♂, 1♀, same except 22.VIII.1968 (J. E. Hafernik). 1♂, Ft. Davis State Pk., 23.VIII.1969 (Board and Hafernik). 2♂♂, 1♀, Cameron Co., Brownsville, 12.VI.1968 (V. V. Board). 1♀, same except 12–14.VI.1969. 1♀, Seguin, 9.V.1964 (J. C. Schaffner). 1♀, Brewster Co., 9 mi W Alpine, 17.VIII.1969 (at light) (J. C. Schaffner). 1♂, 1♀, Basin, Big Bend Nat'l Pk., Brewster Co., 14.VII.1950 (Ray F. Smith). 1♂, 1♀, Chisos Mts., Big Bend Park, 4.VI.1942 (H. H. Scullen). 2♂♂, 3♀♀, Shafter, 6.VIII.1964 (H. R. Burke and J. Apperson). 1♂, 1♀, Hildago Co., Bentsen-Rio Grande St. Pk., (at light) 10.VI.1975 (R. Turnbow). 6♂♂, 9♀♀, Rio Grande State Park, Mission, 3.II.1964 (M. H. Sweet). 1♂, same except 10.VI.1966. 2♂♂, 4♀♀, Mission, 29.V.1965 (M. H. Sweet). 1♂, Pine Springs, Culberson Co., 18.VIII.1970 (C. W. O'Brien). 1♀, College Station, Brazos Co., 9.X.1964 (M. H. Sweet). 1♂, 1♀, Palo Duro Canyon St. Park, Randall Co., 31.VII.1965 (M. H. Sweet). 1♂, 1♀, Sinton, 31.VIII.1964 (M. H. Sweet). 1♀, Uvalde Co., Sabinal (black light), 28.VI.1964 (D. R. Smith & C. W. Baker). MEXICO: 1♂, Jalisco, Puerto Vallarta, 11–15.VI.1963 (P. R. Grant). 1♀, "Nog. 65069, 14585, 28.VIII.1946 (with bamboo stalks)." 1♀, Zacatecas Concepcion del Oro, 8.VII.1983 (at light) (Kovarik, Harrison, Schaffner). 5♂♂, 3♀♀, Durango, Nombre de Dios, Rio Melones, 17.VIII.1977 (H. Brailovsky). 3♂♂, Tamaulipas, CD. Victoria, 17.XI.1977 (H. Brailovsky). In American Museum of Natural History, California Academy of Sciences, California Department of Food and Agriculture (Sacramento), Texas A&M University, University of California at Berkeley, University of California at Davis, Instituto de Biologia Universidad Nacional Autonoma de Mexico, United States National Museum, P. D. Ashlock, D. Engleman, G. G. E. Scudder, A. Slater, and J. A. Slater collections.

Discussion. This species resembles the much more elongate *depicturata* in color. As in that species, the degree of differentiation between the pale and dark areas can be quite variable. Frequently the oblique pale vittae on the scutellum are not confluent posteriorly as they are on the holotype. In dark specimens the longitudinal rays on the posterior pronotal lobe are strongly developed. On such specimens the lateral pronotal rays form a "loop," as they do in many species of *Ozophora,* but the central dark ray does not have a pale median line. In a few specimens the distal end of the

second antennal segment is darkened, as is the third. The membrane varies from almost completely pale (only the base darkened) to almost completely dark with only the apex pale.

Although this species is clearly a member of the *picturata* complex, its pale coloration may cause it to be confused with *O. depicturata*. *O. salsaverdeae* can readily be distinguished from *depicturata* by the uniformly dark fourth antennal segment, and by its shorter stouter body.

Ozophora occidentalis, new species

Description. General form and color as in *salsaverdeae*. Antennal segments I and II uniformly yellow, segment III becoming dark chocolate brown on distal end; segment IV with distal three-fourths chocolate brown strongly contrasting with a narrow basal white or pale yellow annulus. Indistinct dark rays present on posterior pronotal lobe. Scutellum dark brown with strongly contrasting oblique vittae, latter not confluent posteriorly. Hemelytra colored as in *salsaverdeae,* apex of corium with a conspicuous dark macula, lacking a crimson colored apex.

Body vestiture and shape including widened area of corium, shape of metathoracic scent gland auricle, fore femoral spines and relative length of labium as in *salsaverdeae*. Length head 1.0, width 0.90, interocular space 0.48. Length pronotum 0.92, width 1.44. Length scutellum 0.82, width 0.76. Length claval commissure 1.0. Midline distance apex clavus-apex corium 1.20. Midline distance apex corium-apex membrane 0.80. Length labial segments I 0.84, II 0.88, III 0.64, IV 0.44. Length antennal segments I 0.70, II 1.46, III 1.10, IV 1.14. Total body length 5.76.

Holotype. ♂, CALIFORNIA: Los Angeles County, Glendale, 30.VIII.1978 (S. Thurston). In American Museum of Natural History.

Paratypes. CALIFORNIA: 5♂♂, 10♀♀, same data as holotype. 1♂, 2♀♀, N Fork, San Antonio River, 0.7 mi S Indian Ranger Station, Monterey Co., 29.IV.1961 (E. Lindquist). 2♀♀, Carrville, Trinity Co., 20.VI.1951 (E. C. Van Dyke). 2♂♂, 1♀, Trinity Co., Douglas City, 21.VI.1977 (T. R. Haig). 1♂, 3♀♀, Trinity Co., Douglas City, 23.I.1980 (T. R. Haig). 2♀♀, Trinity Co., Del Loma, 6.X.1977 (*Alnus* duff) (T. R. Haig). 1♂, 11♀♀, Trinity Co., Del Loma, 23.II.1978 (T. R. Haig). 1♂, 2♀♀, Shasta Co., 3 mi. S Castella, 14.V.1980 (from oak duff) (T. R. Haig). 1♂, 1♀, Shasta Co., Redding, 1.III.1970 (T. R. Haig). 1♂, same except 1.VII.1974. 1♀, same except 1.IV.1979. 1♂, same except 11.VI.1979. 1♂, Shasta Co., Buckhorn Summit, 18.IV.1981 (T. R. Haig). 1♂, 1♀, same except 9.V.1982. 1♂, 2♀♀, 11 mi W Redding, Shasta Co., 21.XII.1966 (J. S. Buckett, M. R. & R. C. Gardner). 1♀, Riverside Co., Hwy. 395, 55 mi SW Riverside, 2.III.1956 (I. Newell). 1♂, 2♀♀, Davis, Yolo Co., 1.VII.1970 (S. R. Sims). 1♀, Davis, 7.IX.1942 (R. L. Usinger). 1♀, Santa Barbara, Santa Barbara Co., 1967 (V. Roth). 1♂, Colton, 13.I.1910 (G. R. Pilate). 1♂, Wildcat Cyn., San Diego Co., 28.IV.1962 (S. C. Williams). 1♀, Alum Rock Park, Santa Clara Co., 5.IV.1957 (F. Santana). 1♀, Santa Clara Co., 8 mi S Palo Alto, 19.IV.1976 (oak litter) (Fred G. Andrews). 1♂, Santa Cruz Mts. (Koebele Collection). 1♀, Catalina I., 28.IV.—(Parshley Collection). 1♂, Carmel, 4.X.1928 (L. S. Slevin). 1♀, UC Hopland Fld. Sta. nr. H.Q. 880′, Mendocino Co., 22.V.1969 (malaise trap) (W. J. Turner). 1♂, San Juan Ht. Sp. (under dead bark). 11♂♂, 2♀♀, Butte Co., 4.XII.1972 (T. R. Haig). 7♂♂, 8♀♀, Butte Co., Chico, 2.V.1975 (T. R. Haig). 20♂♂, 19♀♀, Los Angeles Co., N Hollywood, 28.IX.1978 (I. Hoodkiss) ("Ex. Home" "78562"). 11♀♀, Contracosta Co., Moraga, 1–8.XII.1980 (D. Denning).

1♀, Contracosta Co., Moraga, 10–15.IX.1981 (D. Denning). 4♂♂, 2♀♀, Glenn Co., Butte City, 21.X.1975 (T. R. Haig). 3♂♂, same except 23.X.1975. 1♂, 9♀♀, Humboldt Co., Berry Summit, 17.XII.1973 (oak duff) (T. R. Haig). 1♀, Santa Paula, 16.II.1957 (W. E. Simonds). 1♂, Stanislaus Co., La Grange, 31.V.1970. 1♂, San Diego Co., 1 mi E Leucadia, 8.VII.1979 ("berlese from under oak") (K. W. Cooper). 1♀, Fresno Co., Fresno, 28.VI.1967 (C. Ferris). OREGON: 1♂, Yamhill Co., IV.1935. 2♀♀, 5 mi S Eugene, Fox Hollow Rd., Lane Co., 27.XI.1959 1,000 ft (D. R. Smith). 1♀, Nuddy Valley, Yamhill Co., 26.V.1957 (K. McKay-Fender). 2♂♂, 2♀♀, McMinnville, Yamhill River, 30.V.1958 (K. McKay-Fender). 1♀, McMinnville, 13.V.1957 (K. McKay-Fender). 1♀, McMinnville, 8.I.1958 (K. M. Fender). 1♀, 1 mi W Curtin, Douglas Co., 27.XI.1959 750' (David R. Smith). 1♀, Corvallis, Benton Co., 7.X.1967. 1♂, Corvallis, Benton Co., 13.I.1960 garden litter (S. Radinovsky). 2♂♂, 1♀, hills NW Corvallis, Benton Co., 22.III.1958 (under bk. debris) (John D. Lattin). 3♂♂, 2♀♀, Scott's Hill 1 mi SW Corvallis, Benton Co., 10.III.1960 (moss & ground litter) (J. D. Lattin). 1♀, Slough 10 mi S Corvallis, Benton Co., 22.XII.1957 (ex. oak leaf litter) (B. Ainscouh). 1♀, Corvallis, Benton Co., 8.IV.1961 (ex. *Salix*). 2♂♂, S side Coffin Butte, Benton Co., 15.I.1959 (sod sample) 500' (John D. Lattin). 1♂, Coffin Butte, 10 mi N Corvallis, 9.I.1958 (oak litter top of butte) (J. D. Lattin). 1♀, same except 9.I.1958 (bullrush litter). 2♂♂, same except 15.I.1959, 300' (litter sample) (S. Radinovsky). 6♂♂, 2♀♀, Corvallis, 7.XI.67 (Paul Oman). 1♀, Corvallis, Oak Creek, 17.I.1959 (flood litter) (S. Radinovsky). 1♂, Corvallis, above Country Club, 31.X.1958 (ground litter) (John D. Lattin). 2♀♀, McDonald Forest, N of Corvallis, 3.XI.1949 (V. Roth). 1♀, 12 mi S Corvallis, 13.III.1949 (in moss) (V. Roth). 1♀, Corvallis, 13.I.1952 (on willow in trap) (V. Roth). 1♀, Sexton Mt. N of Grant Pass, Jackson Co., 26.V.1962 (K. M. Fender). 3♂♂, Spenser's Butte, 2 mi S Eugene, Lane Co., 23.XI.1959 (John D. Lattin). 2♂♂, 2♀♀, Creswell, 530', Lane Co., 27.XI.1959 (ash litter) (David R. Smith). 2♂♂, 2♀♀, 3 mi E Lacomb, Crabtree Gd. Stn., Linn Co., 13.XII.1957 (oak litter) (J. D. Lattin). 1♂, Wasco Co., Sorosis Park the Dalles, 23.X.1968 (oak litter) (E. M. Fisher). NEVADA: 2♀♀, Reno, Washoe Co., 21.X.1958 (John Locke). BRITISH COLUMBIA: 1♂, Penticton, 22.IX.19— (W. Downes). 1♂, McKinney Rd. 1 mi E Oliver, 3.VI.1958 ("Malt trap") (H. & A. Howden). In American Museum of Natural History, United States National Museum, California Academy of Sciences, California Department of Food and Agriculture (Sacramento), University of California (Berkeley and Davis), University of British Columbia, Oregon State University, P. D. Ashlock, G. G. E. Scudder, and J. A. Slater collections.

Discussion. There is very little variation in the type series other than degrees of intensity of the dark coloration.

Although the biology has not been studied collection records suggest an association with oak litter.

Ozophora depicturata Barber

Ozophora depicturata Barber, 1928:266–268.

Discussion. Barber's original description of *depicturata* is detailed and is not repeated here. The transverse dark hemelytral fascia is usually very faint and at least partially obsolete in many Arizona specimens. The basal white annulus of the fourth antennal segment is stated by Barber to occupy the "basal half" of the segment. In

material examined (including two paratypes) it actually occupies only the basal one-third. Barber's discussion of relative lengths and widths are a little misleading since he apparently did not measure most areas. He says that the third and fourth antennal segmenta are subequal (but actually the fourth is longer than the third) and that the third and fourth segments are each "about" one-fourth shorter than the second segment (they are considerably longer than that—see measurements below). Barber states that the anterior pronotal lobe is about twice the length of the posterior. This must be a *lapsus* as the reverse is true. Sometimes only three ventral fore femoral spines are present.

Measurements (from female paratype "Huachuca Mts. Ariz. 26.VII.1905"): Length head 1.16, width 1.10, interocular space 0.50. Length pronotum 1.24, width 1.90. Length scutellum 1.14, width 0.98. Length claval commissure 1.10. Midline distance apex clavus-apex corium 1.80. Midline distance apex corium-apex membrane 1.32. Length labial segments I 1.20, II 1.30, III 1.06, IV 0.50. Length antennal segments I 0.86, II 2.12, III 1.72, IV 1.90. Total body length 7.52.

Barber noted that Arizona specimens in his type series were paler than those from southern California, and our observations support this. Most Mexican and Texas specimens have relatively strongly contrasting markings. In these specimens the transverse hemelytral fascia is strongly differentiated and the pale macula at the inner corial angle contrasts strongly with the dark surrounding surface. In some specimens, dark rays are visible on the posterior pronotal lobe. The median ray anteriorly usually has a very narrow median pale streak. The antennal coloration is almost constant. The first and second segments are uniformly pale, the third segment blackish-brown on the distal end and the fourth segment dark with a prominent white basal annulus.

Barber took specimens by sifting wood rat nests in both California and Arizona. Presumably the insects feed on the seeds present in the litter.

Distribution. Although previously known only from southern California and Arizona, *depicturata* has a much wider range extending into Texas and Mexico. I have also examined several specimens from Guatemala which are either conspecific or represent a very closely related species.

Material examined. ARIZONA: 1♀, Madera Canyon, Santa Cruz Co., 10.VII.1963 4,880 ft (V. L. Vesterby). 2♂♂, same except 11.VII.1963. 2♂♂, same except 12.VII.1963. 1♂, same except 13.VII.1963. 2♂♂, 4♀♀, same except 15.VII.1963. 1♀, same except 18.VII.1963. 1♂, 2♀♀, same except 23.VII.1963. 1♂, 3♀♀, same locality, 5–6.IX.1970 (black light) (E. A. Kane). 1♂, 1♀, American Museum South West Research Station, 5 mi W Portal, Cochise Co., 5,400 ft, 28.VI.1960 (J. M. Linsley). 1♀, Stewart Camp 1 mi S Portal, Cochise Co., 18–20.VII.1971 (black light) (J. T. Doyen). 1♀, Portal, Cave Creek Ranch, 22.VIII.71 (E. G. Linsley). 1♀, same except 29–30.VIII.1971. 4♂♂, 4♀♀, Molino Basin, St. Catalina Mts., Pima Co., 2.VIII.1970 (J. Powell, P. Rude). 2♂♂, Pepper Sauce Canyon, Santa Catalina Mts., 15.VIII.1924 (E. P. Van Duzee). 1♂, same except 16.VIII.1924. 3♂♂, 14 mi E Oracle, 24.VIII.1924 (E. P. Van Duzee). 1♂, Patagonia, 1.VIII.1924 (E. P. Van Duzee). 1♂, same except 2.VIII.1924. 2♀♀, Carr Canyon, Huachuca Mts., 7.VII.1930 (J. O. Martin). 1♂, same except 5,400', 7.XI.19?5 (C. W. O'Brien). 1♀, Bryant, Santa Catalina Mts., 10.I.1940. 1♀, same except 28.VI.1940. 1♀, Sabino Canyon, Santa Catalina Mts., 11.VII.1957 (C. W. O'Brien). 1♂, same except 15.IX.1964 (L. & C. W. O'Brien). 1♀, Globe, 18.VII.1933 (Parker). 1♀, Cochise Stronghold, Dragoon Mts., 7.VII.1958 (C. W. O'Brien). 1♀, White Rock Cp., Pena Blanca Lake, Santa Cruz Co., 7.VII.1958 (L. & C. W. O'Brien). 1♂, Nogales,

20.IX.1933 (H. S. Gentry). 1♀, Cave Creek, Chiricahua Mts., Cochise Co., 5–6,000 ft, 25.VIII.1927 (J. A. Kusche). 1♀, Gila Co., Pinal Mts. 5,500 ft, 13–15.VIII.1977 (black light) (R. P. Allen, Duffy). CALIFORNIA: 1♀, Tanbark Flat, Los Angeles Co., 8.VI.1950 (B. Adelson). 1♂, Aliso Canyon, 6 mi SW New Cuyama, Santa Barbara Co., 9.VII.1965 (D. Bragg). 1♂, 8 mi N Ojai, North Fork Matilija Creek, Ventura Co., 2,000 ft, 21.V.1981 (L. Herman). 1♂, same except 9.VII.1965 (E. M. Omi). 1♂, 2♀♀, 4 mi W Los Prietos, Santa Barbara Co., 1.IX.1968 (white light) (P. & S. Opler). 1♂, Maricopa Co., 3 mi S Sunflower on Hwy 87, 7.IX.1983 (black light trap) (W. H. Cross). 2♀♀, Trinity Co., Del Loma, 6.X.1977 (berlese, *Alnus* duff) (T. R. Haig). 1♂, San Bernardino Co., 2 mi E Mt. Home Village, 7.X.1981 (berlese *Neotoma* nest under oak) (K. W. Cooper). 1♀, Kern Co., Lake Isabella, 4.7 mi S Woffold Heights, 25.X.1980 (A. R. Hardy). TEXAS: 1♂, Texas Experiment Station, Dimmit Co., 1.IV.1936 (S. E. Jones). 1♀, same except 18.III.1942. 1♂, Lange's Hill, Gillespie Co., 5.VI.1960 (Board & Hafernik). 1♀, Taylor, 11.IV.1965 (J. E. Hafernik). 1♀, Bryan, 13.IV.1965 (J. C. Schaffner). 1♀, Eagle Pass, 8.VIII.1959 (R. B. Selander, J. C. Schaffner). 1♀, Garner St. Park, Uvalde Co., 11.VI.1965 (M. H. Sweet). 1♀, Presidio, 8.VII.1968 (J. E. Hafernik). MEXICO: 1♂, Jalisco, Guadalajara, 20.XII.1963 (M. J. Tauber & C. A. Toschi). 14♂♂, 23♀♀, Nuevo Leon, 15 mi W Linares, 1–2.VII.1973 (Mastro & Schaffner). 34♂♂, 20♀♀, same except 27.VII.1978 (at light) (Plitt & Schaffner). 1♂, 4♀♀, Nuevo Leon 16.5 mi W Linares, 22–24.VII.1977 (R. Peigler, D. Plitt). 12♂♂, 14♀♀, same except 23.VII.1976 (at light) (Peigler, Gruetzmacher, R. & M. Murray, Schaffner). 1♀, Nuevo Leon, 20 mi S Monterrey, 17.XI.1946 (E. C. Van Dyke). 1♀, Morelos, 4.4 mi E Cuernavaca, 27–29.VII.1976 (at light) (Peigler, Gruetzmacher, R. & M. Murray, Schaffner). 2♂♂, 1♀, Morelos, 15.1 mi E Cuernavaca (R. R. & M. E. Murray). 2♂♂, Aguascalientes, 5 mi E Calvillo, 10.VII.1983 (black light) (Kovarik, Harrison, Schaffner). 1♀, Colima, 9 mi NE Comala, 18.VII.1983 (at light) (Kovarik, Harrison, Schaffner). 2♂♂, 5 mi SW C. Victoria, Tamps, 1,100 ft, 10.VI.1963 (Duckworth & Davis). 1♀, Taxco, Guerrero, 14.II.1962 (D. G. Denning). 1♂, Oxacaca, 9 mi N C. Loxicha, 15–16.VII.1973 (Mastro & Schaffner). 1♂, Mich. Tuxpan, 7–8.VII.1965 (Flint & Ortiz). 1♂, Real de Arriba, Temescaltepec, 23.V.1933 (H. E. Hinton & R. L. Usinger). 17♂♂, 19♀♀, Cuiteco Chih., 27.VIII.1969 (T. A. Sears, R. C. Coacher, C. S. Glaser). 1♀, L. Cal., 20 mi S Santo Thomas, 3.VIII.1938. 1♀, Son., Guasaremos Rio Mayo, 30.VII.1935 (L. G. Gentner). 5♂♂, 8♀♀, Las Minas, Vera Cruz, 1,360 m, 6.IX.1977 "noct." (H. Brailovsky). 3♂♂, same except (E. Barrera). 2♂♂, 1♀, Tepoztlan, Morelos, 20.II.1977 (E. Barrera). 1♂, Guanajuato, Guana Juato, 20.XII.1981 (H. Brailovsky). In American Museum of Natural History, California Academy of Sciences, California Department of Food and Agriculture (Sacramento), Instituto de Biologia, Universidad Nacional Autonoma de Mexico, United States National Museum, University of California (Berkeley), University of California (Davis), University of Connecticut, Texas A&M University, P. D. Ashlock, H. Brailovsky, and J. A. Slater collections.

Ozophora angustata Barber

Ozophora angustata Barber, 1948:202–203.

Discussion. Both *angustata* and *depicturata* are relatively elongate, slender insects and are almost completely pale yellow in color. They may be readily separated by the condition of the lateral margins of the anterior pronotal lobe. In *O. angustata,*

these lateral margins are narrowly but acutely carinate whereas in *depicturata* they are obtusely ridged (or "calloused") as they are in most species of *Ozophora*. The head of *angustata* is also distinctive. Not only is it more strongly convex on the vertex but the length of the head anterior to the eyes is twice the length of an eye whereas in *depicturata* it is only 1¾ times the eye length.

The holotype (and only known specimen) is submacropterous. The membrane is well-developed but extends only over the anterior ⅔ of abdominal tergum seven. This submacroptery may account for the much narrower pronotum of *angustata* but will not account for the sharply carinate rather than "calloused" lateral pronotal margins. Length-width *angustata* 0.98–1.26 (ratio 1.29); length-width *depicturata* (male paratype), 1.12–1.66 (ratio 1.48).

Barber's excellent original description requires a few modifications. He stated that only two fore femoral spines are present but there are four. His statements concerning labial length may be a little misleading as the head of the holotype is somewhat exerted. Barber stated that the labium extends "just past posterior coxae" which is true. However, with the head in "normal" position the labium probably extends well over the second visible sternal segment. This also suggests that the first labial segment may reach the base of the head rather than only slightly beyond the posterior margin of the eye as stated by Barber. Measurements of the holotype are as follows: Length head 1.06, width 0.86, interocular space 0.52. Length pronotum 0.98, width 1.26. Length scutellum 0.72, width 0.58. Length claval commissure 0.96. Midline distance apex clavus-apex corium 1.20. Midline distance apex corium-apex membrane 0.50. Midline distance apex membrane-apex abdomen 0.86. Length labial segments I 1.10, II 1.14, III 1.02, IV 0.50. Length antennal segments I 1.06, II 2.42, III and IV missing (Barber's original description states that segment IV is slightly longer than segment II). Total body length 6.40 (Barber says 7.65).

This must be a very rare or localized species as despite a considerable amount of material available from Texas it remains known only from the holotype from "Big Bend Park, Brewster Co., Texas."

Ozophora consanguinea (Distant)

Davila consanguineus Distant, 1893:395.
Ozophora consanguinea Uhler, 1894:186–187.
Peggichisme consanguinea Sweet, 1967:223.
Ozophora consanguinea Slater, 1983:25–26.

Discussion. This is a large variegated species readily recognizable by the acute explanate lateral margins of the pronotum. It is closely related to *unicolor* Uhler, much more so, in my opinion, than is *unicolor* to *Balboa ampliata* (see discussion of latter) despite the similarity in color of the two latter species. Both *consanguinea* and *unicolor* have acute lateral pronotal margins that are deeply sinuate, elongate posteriorly curving metathoracic scent gland auricles and prominent white annuli on the fourth antennal segments.

Ozophora consanguinea was synonymized with *picturata* Uhler by Van Duzee (1916) but resurrected by Sweet (1967) at the same time that he raised *Peggichisme* Kirkaldy from synonymy. Ashlock and Slater (1982) concluded that the acutely sharpened pronotal margin was too variable a feature to warrant its use for generic recognition and reduced *Peggichisme* to junior synonymy with *Ozophora*.

Ozophora consanguinea was first reported from the United States by Slater (1983) based on Texas specimens from Laredo, Dimmit Co., Winter Haven, Cameron Co., and Harlingen.

This species is quite variable in color and may represent a complex of closely related taxa. Sweet, in fact, has placed labels on two of the Texas specimens indicating he believed they represent a new species. I have examined a long series extending from Mexico through Central America, and into northern South America. Texas specimens have chiefly dark brown hemelytra with two large pale yellow macula on each corium, one at the level of the claval commissure, the other at the level of the middle of the apical corial margin. Most Central American specimens are paler, some as pale as *picturata.* However, there are many gradations between and we have examined specimens as dark as those from Texas from Belize, Guatemala, El Salvador, Panama and Mexico.

Ozophora maculata Slater and O'Donnell

Ozophora maculata Slater and O'Donnell, 1979, 52:167–170.

Discussion. This is a very small species (less than 4 mm) and readily separable from all other southwestern United States species by size alone. It usually has a complete transverse corial fascia but this fascia may be reduced or absent.

The original description of *maculata* included records of specimens from Santa Cruz and Nogales, Arizona.

Material examined. ARIZONA: 1♂, Duncan, 21.VII.1956 (swept alfalfa) (T. Dees). 1♂, Patagonia Sta. Cruz, 9.VIII.1956 (C. W. O'Brien). 1♂, 1♀, Patagonia. BAJA CALIFORNIA: 1♀, Triunfo, 7.VII.1938 (Michelbacher and Ross). In California Academy of Sciences, P. D. Ashlock and J. A. Slater collections.

Ozophora unicolor Uhler

Ozophora unicolor Uhler, 1894, (2):4:242–243.

Discussion. This species was originally described from two localities in Baja California, Mexico (San Jose del Cabo and Cape Lucas). Despite statements of "California" by Lethierry and Severin (1894), Banks (1910), Van Duzee (1916, 1917, "?") and Torre-Bueno (1946) the species apparently remains known only from Baja California and appears to be endemic there.

In his original description Uhler did not designate a holotype but stated in the introduction to the article that the types of species described in that paper were deposited in the California Academy of Sciences. All of the specimens of *unicolor* at present in the California Academy collections bear much later dates (1938 and 1941). In the National Museum of Natural History (USNM) in Washington are 5 female specimens all labeled "P. R. Uhler collection." Four of these bear the locality "L Cal.," one of these has a red label saying "Type No. 25857 USNM" and an additional label in Uhler's handwriting saying "*Ozophora unicolor* Uhler." The other three specimens bear similar red labels but with the notation "Paratype." The fifth specimen also bears red paratype and Uhler collection labels, but the locality label reads "Cap St. Lucas." It seems evident that despite Uhler's statement, the types were not returned to the California Academy of Sciences and the Washington material is the type series. Despite the label, no valid "type" has been fixed. The specimen bearing

the label "type" as described above is here designated as Lectotype. The other "paratypes" become paralectotypes.

O. unicolor is a very distinctive species. It is almost entirely dark brown, including the entire membrane. There is a contrasting yellow stripe along each lateral corial margin and along the inner margin of each clavus. The first and second antennal segments are dull yellow as is most of the third segment. The latter is infuscated on the distal end. The fourth segment is chocolate brown with a broad subbasal white annulus.

O. unicolor appears to be most closely related to *consanguinea.* It shares with that species the sharply carinate, deeply sinuate, and explanate lateral pronotal margins, and the elongate tapering posteriorly curving metathoracic scent gland auricle. Other descriptive features are as follows: (measurements from lectotype) Head short, moderately declivent; vertex strongly convex; tylus extending anteriorly only to proximal ⅓ of 1st antennal segment. Eyes large, moderately produced. Length head 1.0, width 1.12, interocular space 0.56. Pronotal calli strongly convex, smooth, confluent mesally; lateral pronotal margins only shallowly concave. Length pronotum 1.24, width 2.08. Length scutellum 1.36, width 1.12. Length claval commissure 1.16. Midline distance apex clavus-apex corium 1.72. Midline distance apex corium-apex membrane 1.28. Metathoracic scent gland auricle elongate, acute, strongly curving posteriorly. Labium attaining or nearly attaining metacoxae. Length labial segments I 1.04, II 1.00, III 0.76, IV 0.48. Length antennal segments I 0.84, II 1.72, III 1.44, IV 1.76. Total body length 7.36.

Additional material examined. LOWER CALIFORNIA: 2♂♂, 1♀, Todos Santos, 10.X.1941 (Cross and Bohart). 1♂, 1.38 mi NE of Coomon Du T. S., 9.VII.1937 (R. E., J. V., A. E. Ryckman & D. Spencer). 1♂, 215 km N of La Paz, 11.VII.1957 ("in shoe") (R. E. Ryckman). 3♂♂, 3♀♀, 15 mi N El Refugio, 4.VII.1938 (Michelbacher and Ross). 1♀, 157 km NW La Paz, 11.VII.1957 (R. E., J. V., A. E. Ryckman and D. Spencer). 1♂, Agua Caliente, Cape Region, 18.X.1941 (Ross and Bohart). In P. D. Ashlock, California Academy of Sciences, and J. A. Slater collections.

In the original description Uhler mentioned that the head is broadly grooved along the midline, but the head is actually evenly convex. The apparent groove is merely a paler color marking that is present on some specimens. Uhler also says that the "ground surface" is impunctate. However, actually *unicolor* is as punctate as most other species of *Ozophora.* Later in the description Uhler indicates that the surface is punctate. His statement that antennal segments two and three are equal and that segment four is a little shorter must have been merely based on visual observation and is inaccurate (see measurements above).

Although as noted above, *unicolor* is closely related to *consanguinea,* it is of the same color as the southwestern species *Balboa ampliata* Barber. The relationship may be more than a superficial color resemblance as noted in the discussion of *ampliata.*

Balboa ampliata Barber

Ozophora ampliata Barber, 1918:52–53.
Dieuches occidentalis Torre-Bueno, 1946:126–128.
Balboa ampliata Ashlock, 1960:237.

Discussion. This is a large, almost uniformly dark brown species. In general appearance it closely resembles *Ozophora unicolor* Uhler.

The systematic position is most interesting. Eyles (1969) has summarized its systematic history. He noted that Ashlock (1960) removed it from *Ozophora* to *Balboa* because of the broad lateral pronotal carina and the stridulitrum along the lateral margin of the front wing, and that Torre-Bueno (1946) redescribed it as a new species of *Dieuches.* While it is true that Ashlock used the pronotal carina as one of the distinguishing features, the presence of the stridulitrum along the lateral corial margin is probably of more definitive importance (see Ashlock and Slater, 1982). However, the importance of such stridulatory structures as criteria for generic recognition is certainly open to question. An abdominal stridulitrum is known to have developed independently several times not only within a tribe (Harrington, 1980) but in such different tribes as the Myodochini and Ozophorini. Slater (1983) has suggested that within the Ozophorini the genus *Lygofuscanellus* Scudder recognized on the basis of the abdominal stridulitrum would probably be polyphyletic if all Western Hemisphere ozophorines having this feature were placed in the same genus. He has described a new species of *Ozophora* with an abdominal stridulitrum. In fact the corial margin wing stridulitrum has itself evolved independently several times (Ashlock and Lattin, 1963).

Despite this we believe that *B. ampliata* is best retained, at least for the present, in *Balboa.* It is, however, quite isolated from the other two species of *Balboa* (only *variabilis* Distant and *germana* (Distant) have been described but there are several similar undescribed Central American species). The resemblance of *ampliata* to *Ozophora unicolor* is chiefly one of color. The shape of the metathoracic scent gland auricle is also similar but not more so than that between *B. ampliata* and *B. variabilis.* *B. ampliata* can be distinguished from *O. unicolor* as follows: (1) *B. ampliata* has the above-mentioned corial stridulitrum. (2) In *ampliata* the explanate lateral margins of the pronotum are evenly, arcuately curved whereas in *unicolor* the lateral pronotal margins are deeply sinuate. (3) *B. ampliata* has a uniformly dark fourth antennal segment, while *O. unicolor* has a broad, subbasal, white annulus present. (4) The metathoracic evaporative area occupies only the inner half of the metapleuron in *ampliata* but covers the inner ⅔–¾ in *unicolor.* (5) The apex of the scutellum is uniformly dark brown and concolorous with the remainder of the scutellum in *ampliata* (occasionally slightly paler) whereas in *unicolor* the extreme apex is usually white. (6) *B. ampliata* is a considerably larger and more robust species.

Nevertheless the overall similarity is such that Barber (who originally described *ampliata*), determined a typical specimen as *Ozophora unicolor.*

In his original description of *ampliata* Barber noted its similarity to *unicolor* and stated that *ampliata* was "generally paler." I have not found this to be true.

Nothing is known of the biology of *ampliata,* but it appears to be a montane species in southern Arizona.

Eyles (1969) gives excellent illustrations of the dorsal surface and of the fore femur.

Distribution. Barber's holotype was from "Arizona" without definite locality, his paratypes are from Carr Canyon, Huachuca Mountains. Torre-Bueno's holotype of *Dieuches occidentalis* was from Madera Canyon, Santa Rita Mountains, Arizona (5,000 ft).

Material examined. ARIZONA: 1♂, 5 mi W Portal (S.W.R.S.), 5,400 ft, 15.VII.1956

(C. and M. Cazier). 1♀, same except 23.VIII.1956 (M. Cazier). 2♂♂, 1♀, SW Res. Sta., 2.VIII.1956 (M. J. Westfall Jr.). 1♀, Santa Catalina Mts., 5,000 ft, VII.1938 (Bryant). 2♂♂, 4 mi SW Forestdale, 23–24.VIII.1952 (pine forest) (H. B. Leech). 1♂, Pine, 3.IX.1937 (R. P. Allen). 2♀♀, Show Low, Navajo Co., 21.VIII.1952 (B. Malkin). 1♀, Cochise Co., 5 mi W Portal, 26.VIII.1976 (black light) (Fred G. Andrews). 1♀, Cochise Co., 12 mi S Sierra Vista, 8–10.VIII.1977 (R. P. Allen, G. C. Duffy). 4♂♂, 6♀♀, Cochise Co., San Rafael Valley, 10–11.VIII.1977 (black light) (R. P. Allen & G. C. Duffy). 1♀, Cochise Co., Rustler Park, 25.VII.1982 (Fred G. Andrews). 1♂, Pima Co., Madera Canyon, 6.IX.1970 (E. A. Kane). 2♂♂, 3♀♀, Santa Cruz Co., Madera Canyon, 22.VIII.1971 (black light) (E. A. Kane). 4♂♂, 5♀♀, Gila Co., Pinal Mts. 5,500 ft, 13–15.VIII.1977 (black light) (R. P. Allen, Duffy). NEW MEXICO: 1♂, Bear Trap Camp, 28 mi SW Magdalena, Socorro Co., 8,500 ft, 20.VII.1964 (F. P. and M. Rindge). In American Museum of Natural History, California Academy of Sciences, Texas A&M University and J. A. Slater collections.

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AGRENIA LAMELLOSA, A NEW SPECIES OF COLLEMBOLA (ISOTOMIDAE) FROM PENNSYLVANIA

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Abstract.—The new species differs from the six other nearctic members of the genus by the strongly developed ventral lamella of the mucro. Epitoky is reported in reproductive males. The nearctic distribution of *Agrenia* appears to have two components: A western montane species complex and a corresponding eastern complex which is still largely unknown. The new species is the first verified eastern species. A second undescribed species was seen in an old sample from North Carolina.

The genus *Agrenia* Börner, 1906, was revised by Fjellberg (1986). The formerly monotypic genus proved to be a complex of several species. Five new species were described from North America in addition to the classical *bidenticulata* (Tullberg, 1876): *agilis, atroviridis, cyanura, polymorpha,* and *riparia.* Within the U.S., *bidenticulata* and *riparia* were reported from Alaska and *cyanura* from Oregon. The other three nearctic species appeared in Alberta and/or British Columbia.

Christiansen & Bellinger (1980), referring to *bidenticulata* s.l., reported the taxon from the following states in the east: New York, Connecticut, Pennsylvania, Indiana, Tennessee, North Carolina, and Alabama, and from the following western states: Colorado, Utah, Wyoming, Idaho, Montana, Oregon, Washington, Alberta, British Columbia and Alaska. There are several additional records from arctic Canada. Thus, the distribution of the genus seems to cover the mountainous states in the west and in the east, being absent from the great plains (the record from Indiana refers to a juvenile specimen and should be verified). Probably a number of still undescribed species are involved.

Through the kind assistance of Dr. Robert D. Waltz, I obtained a sample of *Agrenia* collected in a stream in Centre County, Pennsylvania. It proved to be an unknown species which is described below.
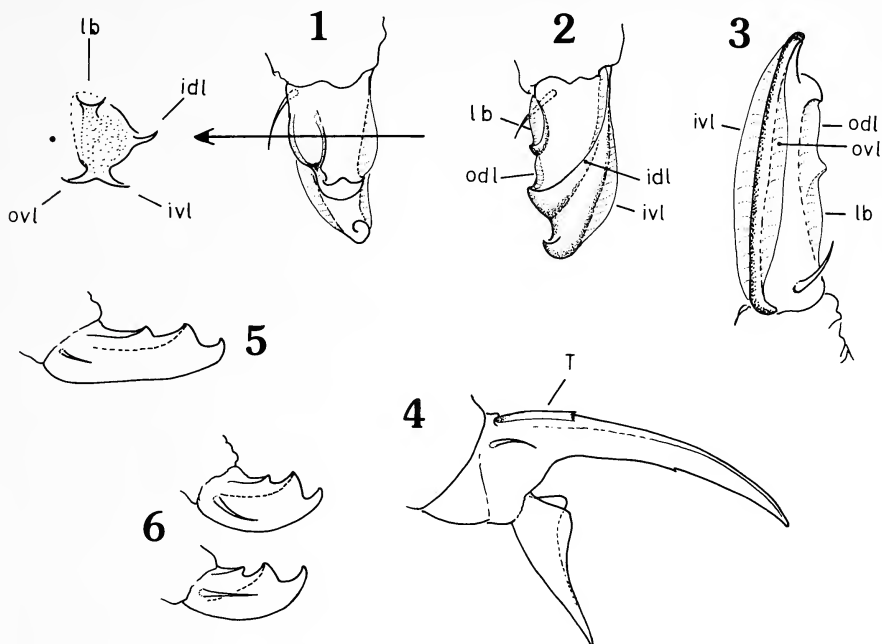
Agrenia lamellosa, new species
Figs. 1–5

Type material. Holotype (slide), USA, Pennsylvania, Centre Co., Slab Cabin Run, 6 km SW State College. 15–16.vii.1981. Drift net sample. P. H. Adler & R. W. Light leg. In USNM.

Paratypes (all slide specimens from the type locality). 3 in USNM, 3 in CNC, 1 in BMNH, 1 in TM.

Description. Size 1.8 mm (largest specimen), reproductive adults from 1.2 mm.

Color pale blue gray, tergites of thorax and anterior abdomen slightly darker. Antennae, eye-spots, central head-spot and neck region bluish black (specimens were stored 6 years in alcohol and probably have faded).

Figs. 1–6. *Agrenia lamellosa* n. sp. 1–3. Lamellary complex of left mucro. lb: Lamella of basal tooth; idl: Inner dorsal lamella; odl: Outer dorsal lamella; ivl: Inner ventral lamella; ovl: Outer ventral lamella. 1. Dorsal aspect, cross section to the left. 2. Dorsal, oblique. 3. Ventral, oblique. 4. Claw complex. T: Tunica. 5. Left mucro, lateral. 6. *Agrenia polymorpha,* left mucro. Two different specimens.

Antennae 1.7–1.9 as long as head diagonal (profile). Head with 8 + 8 ocelli (G and H smaller). PAO oval, subequal to an ocellus. Shape of head normal, not prognathous.

Body with open, uniform hair cover, macrochaetae not developed. Ventral tube with 2–5 frontal setae, 8–9 lateral, and more than 20 caudal setae. Tenaculum with 15–20 setae. Claws slender, tunica short (Fig. 4). Claw index (cf. Fjellberg, 1986) 2.6–3.2. Furca 2.0–2.2 as long as head diagonal. Dens 1.6–2.0 as long as manubrium. Mucro strong, with subequal apical and antapical teeth (Fig. 5). Ventral edge straight or gently curved. A short lateral seta present. Mucronal lamellae strongly developed, especially the outer and inner lamellae running along the ventral edge (Figs. 1–3).

Reproductive males slightly epitokous, with shortened hairs on Abd. 5–6, otherwise normal.

Discussion. The only other nearctic *Agrenia* species with the mucronal seta present, are *polymorpha* and *bidenticulata.* Both of these species differ from *lamellosa* by having a shorter mucro with strongly curved ventral edge and longer lateral setae (Fig. 6). The broad ventral lamella of *lamellosa* appears to be unique. I have checked *polymorpha, bidenticulata, cyanura, agilis,* and *riparia,* which all have a sharp, narrow ventral keel in the basal half, widening slightly in the apical half. Also the claws of *lamellosa* are more slender than in related species, and the tunica is shorter (Fig. 4).

The proportions of antennae, head and furca fall within the ranges of *polymorpha* and *bidenticulata*. The observed epitoky in reproductive males of *lamellosa* corresponds to the short-haired males of *polymorpha* and *riparia* (Fjellberg, 1986).

At least one other species of *Agrenia* is present in the eastern states. A sample collected by K. Christiansen in 1950 at Winkler's Creek, Watanaya, North Carolina, has individuals which have the same general mucro-shape as *lamellosa,* but the lateral seta seems to be absent. Mucronal lamellae are unclear due to the transparency of the old specimens. The claws are more robust and possess a larger tunica (claw index 2.3). The clearest difference, however, is found in the general hair cover. Whereas *lamellosa* has an uniform cover in the anterior part of the body, the North Carolina specimens have a strikingly "double" hair cover on head, thorax and the first abdominal segments, with mixed short and long setae all over (similar to the Japanese species *pilosa,* see Fjellberg, 1986, fig. 15). A description of this species should be based on freshly collected specimens.

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HOST DISCRIMINATION IN *MONODONTOMERUS OBSOLETUS* FABRICIUS (HYMENOPTERA: TORYMIDAE), A PARASITE OF THE ALFALFA LEAFCUTTING BEE *MEGACHILE ROTUNDATA* (FABRICIUS) (HYMENOPTERA: MEGACHILIDAE)

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Abstract. — An experimental investigation of the host discrimination of *Monodontomerus obsoletus,* a gregarious parasitoid of immature alfalfa leafcutting bees, *Megachile rotundata,* was conducted. Naive or experienced parasitoids distinguished two classes of parasitized hosts from unparasitized hosts, based on the time interval since initial parasitization. Hosts parasitized 72 or more hours before exposure to a second female were rarely superparasitized. Hosts parasitized 24 hours prior to exposure to a second female were usually superparasitized but fewer eggs were deposited in second broods than in first broods. A significant inverse correlation was observed between the size of first and second broods in 24-hour hosts. This suggests that superparasitizing females were able to approximate the size of first broods and adjusted the size of their own broods accordingly.

Ovipositing females of many species of parasitic wasps discriminate between unparasitized hosts and those that have been parasitized by conspecifics (Salt, 1961; van Lenteren, 1981). Parasitized hosts may be distinguished by a pheromone applied during parasitization, by tactile or auditory cues (Arthur, 1981; van Lenteren, 1981) or by some form of "internal marker" (Strand, 1986). Responses to some cues may also be modified by experience: in some species, females with oviposition experience are more likely than naive females to reject parasitized cocoons (van Lenteren and Bakker, 1975; van Lenteren, 1976).

This study reports on host discrimination by *Monodontomerus obsoletus* Fabricius, a torymid parasitoid of immature solitary bees. Among its hosts is *Megachile rotundata* (Fabricius), the alfalfa leafcutting bee, the most important commercial pollinator of alfalfa in the Pacific northwest. To better understand the relationship between this parasitoid and its agriculturally important host, experiments were designed to answer the following questions: (1) Can female *M. obsoletus* distinguish parasitized from unparasitized *M. rotundata*? (2) Do female parasitoids distinguish between hosts that differ in the time elapsed since they were parasitized? (3) Are experienced females more likely than naive females to reject parasitized hosts?

The behavior and biology of *M. obsoletus* has been studied in some detail by Eves (1970), and Hobbs and Krunic (1971), who mistakenly referred to it as *M. obscurus* Westwood (E. E. Grissell, pers. comm.). Briefly, females gain entry to a nest of *M. rotundata* where they immobilize immatures by stinging them through the protective leaf sheath and/or cocoon layers. A variable number of eggs is then deposited between the inner cocoon wall and the host [usually 6–10; Eves (1970) reports a range of 3–51 eggs/host but I have rarely found more than 15]. The eggs hatch in about 36 hours

at 29°C, and non-cannibalistic larvae devour the host in 5–6 days. Adults emerge from the host cocoon at about 20 days. The sex ratio of broods is almost invariably biased towards females and sib-mating is probably the predominant breeding system (Hamilton, 1967). In the laboratory, siblings emerge from the cocoon over a short period of time, and mate almost immediately. Indeed, some females mate with their brothers before emerging from the host (Tepedino, 1988a). After mating, the cycle is recommenced either in the same *M. rotundata* burrow, if unparasitized hosts are available, or in a different one. All immature stages of *M. rotundata* are vulnerable to attack although parasitization of early larval instars is rarely successful.

<center>MATERIALS AND METHODS</center>

All *M. obsoletus* used for experiments were randomly selected from individuals emerging from stock cultures maintained at this laboratory. Prepupae of *M. rotundata* were radiographed (Stephen and Undurraga, 1976) in their cocoons and leaf sheaths prior to use so that obviously dead individuals could be detected and eliminated. Healthy-appearing prepupae were used as hosts one day after their removal from winter storage (4–5°C).

Each of 20 naive female parasites was placed in a clean glass petri dish with three host cocoons for 24 hours at 29°C and 16L:8D photoperiod. Each cocoon represented a different treatment: (1) unparasitized; and parasitized by another *M. obsoletus* female (2) 24 hours earlier and (3) 96 hours earlier. Three hosts were chosen because *M. obsoletus* usually parasitizes three or more cocoons in the first 24 hours after emergence. In another study (Tepedino, 1988b), 28 of 29 females presented with six healthy hosts parasitized 3 or more of them in the first 24 hours. Thus females were expected to parasitize all three hosts offered unless one or more of the treatments were unacceptable. All previously parasitized cocoons were kept at 29°C and 16L: 8D from initial parasitization until presentation to naive females. After 24 hours, females were removed, host cocoons were opened and their contents examined. The presence of both eggs and larvae in a cocoon indicated superparasitism. Because eggs hatch in about 36 hours (Eves, 1970), only those from the first brood in treatments 2 and 3 would have hatched into larvae.

A second group of 10 freshly emerged, naive females were each presented with one healthy, unparasitized cocoon in a glass culture dish at 29°C and 16L:8D photoperiod for 24 hours. The cocoons were then removed, and the wasps held at 25°C in the dark for 72 hours. During this time females were fed a drop of 50% honey solution applied to an unused cigarette filter inserted into a sidearm in the dish. At the end of the 72 hours, females were presented with three experimental cocoons as described above for naive females except that the 96 hour treatment was replaced by a cocoon which had been parasitized 72 hours before. Subsequent treatment was as described above for naive females.

<center>RESULTS</center>

Naive female *M. obsoletus* parasitized 34 of 57 available hosts. [Each of three replicates contained a dead host undetected by radiography. All three were victims of the fungal disease, chalkbrood, *Ascosphaera* (McManus and Youssef, 1984)]. No female parasitized all three hosts; fourteen females attacked two hosts each; six

Table 1.   Mean number of eggs deposited by naive females in unparasitized or parasitized cocoons and the mean number of larvae in the pre-parasitized cocoons. N_L = total number of cocoons with larvae available; N_E = total number of cocoons with eggs.

Cocoon treatment	Mean number (+SD)			
	N_E	Eggs	N_L	Larvae
Unparasitized	18	9.2 (4.8)	—	—
Parasitized 24 hrs	13	5.8 (4.1)	18	8.2 (2.4)
Parasitized 96 hrs	3	5.0 (3.0)	19	10.4 (1.9)

females attacked one host each. As in a previous study (Tepedino, unpublished), females that parasitized two hosts deposited fewer eggs per host (6.9 ± 1.7) than those that parasitized only one host (10.2 ± 4.6) ($t = 2.39$, $P < 0.05$).

Naive females clearly avoided hosts parasitized by conspecifics 96 hours earlier. Of the hosts available (20 unparasitized, 18 parasitized 24 hours earlier, 19 parasitized 96 hours earlier), significantly fewer of those parasitized 96 hours earlier were attacked than those of the other two categories (Table 1, $\chi^2 = 22.8$, df = 1, $P < 0.001$). There was no significant difference in frequency of attack between unparasitized cocoons and those parasitized 24 hours earlier ($\chi^2 = 1.2$, df = 1, $P > 0.25$).

Important differences were detected among host treatments in the number of eggs deposited per host. Although the frequency of attack upon unparasitized hosts and those parasitized 24 hours earlier did not differ, there was a significant difference between them in the number of eggs laid per host (Table 1). Naive females deposited significantly more eggs in unparasitized hosts than in those parasitized 24 hours earlier ($t = 2.02$, df = 28, $P = 0.05$).

Indirect evidence suggests that naive females in the choice experiments parasitized unparasitized hosts before superparasitizing 24- and 96-hour hosts. Each 24- and 96-hour host received its first brood from a single naive female. The number of eggs laid by these females (Table 1, Larvae) thus represent a useful standard against which to compare the number of eggs deposited by naive females in the choice experiments. There was no difference in the size of first broods in 24-hour hosts, 96-hour hosts or unparasitized hosts in the choice experiments (ANOVA, F = 2.26, df = 2,51, $P > 0.10$). This finding, coupled with the significant differences among treatment types reported above, suggests that females attacked unparasitized hosts first, possibly after investigating other available hosts. The data also suggest that superparasitizing females adjusted the number of eggs deposited to the number of eggs already present in the host. There was an inverse relationship between the number of eggs laid by first and second females on 24-hour hosts (Fig. 1), but it was not significant ($r = -0.47$, df = 12, $P = 0.10$).

The behavior of females with a single previous oviposition experience closely resembled that of inexperienced females. Although sample sizes were diminished by the presence of ten moribund but undetected victims of chalkbrood, results were unambiguous: first, all seven unparasitized hosts were parasitized, all six 24-hour hosts were superparasitized, but none of the seven 72-hour hosts were superparasitized. Second, like their naive counterparts, experienced females laid fewer eggs in hosts parasitized 24 hours earlier than in unparasitized hosts (8.2 ± 4.4 vs. 10.3 ±
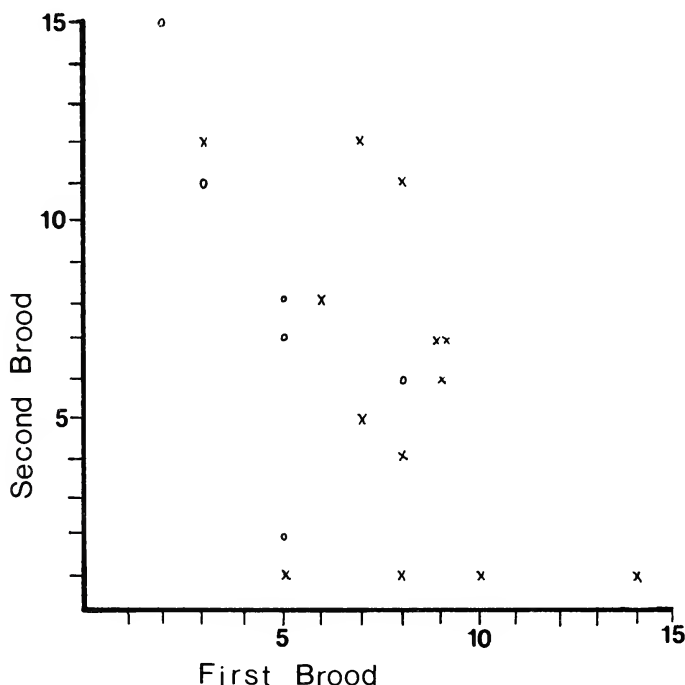
Fig. 1.   The number of progeny from first and second (superparasitism) broods of *M. obscurus* in prepupae of *M. rotundata* ($Y = -0.85x + 12.45$).

2.3) but in this case the result was not significant ($t = 1.11$, df = 5,6, $P > 0.25$). And third, an inverse, but non-significant, correlation was found between the number of eggs deposited by experienced females in 24-hour cocoons and the number of eggs already present in the cocoon (Fig. 1; $r = -0.71$, df = 5, $P = 0.11$). If the results for superparasitism of 24-hour hosts are combined for experienced and naive females, as is permissible because they did not differ in oviposition behavior, then the inverse correlation between the number of eggs laid in first and second broods is significant (Fig. 1; $t = 2.87$, df = 17, $P = 0.01$).

DISCUSSION

Monodontomerus obsoletus may be added to the burgeoning list of hymenopterous parasitoids that distinguish unparasitized hosts from those parasitized by conspecifics. Unlike some other species (van Lenteren and Bakker, 1975; van Lenteren, 1976), discriminatory ability of females was not improved by prior oviposition experience with an unparasitized host.

In general, the results for *M. obsoletus* resemble those for *Nasonia vitripennis* (Walker) (Werren, 1984). In both studies essentially four classes of prospective hosts were distinguished by ovipositing females: (1) unparasitized-acceptable; (2) parasitized-acceptable; (3) parasitized-unacceptable; and (4) unparasitized-unacceptable

(moribund). The obvious difference between hosts of classes 2 and 3 is the time since initial parasitization. For both species a positive relationship was found between percent hosts rejected and the time since the host was first parasitized. Other examples of similar behavior are cited by Strand (1986). In this study, hosts parasitized at least 72 hours before being offered to naive females were superparasitized only rarely, but those parasitized 24 hours earlier were superparasitized almost without exception. Distinctions between host classes may be made by whether feeding larvae are present in the host cocoon or not [in *M. obsoletus* eggs hatch at about 36 hours and first instar larvae begin to feed as soon as they attach to the host (Eves, 1970)], or by the presence of external or internal markers, or a combination of these (Werren, 1984; Strand, 1986). Studies are underway to address some of these questions.

Until recently, the conception of superparasitism as a cost of either inexperience or error was based on the surmise that progeny of superparasitizing females were invariably doomed (Salt, 1961; van Lenteren, 1981). Under such circumstances females would be under strong selective pressure to distinguish unparasitized hosts from those parasitized by conspecifics and to avoid the latter. However, several researchers (van Alphen and Nell, 1982; Charnov and Skinner, 1984; Parker and Courtney, 1984; Werren, 1984; Bakker et al., 1985; Skinner, 1985; Waage, 1986) have recently pointed out that superparasitism is to be expected in some situations. For example, superparasitism is likely to be advantageous when the probability of finding unparasitized hosts is low and there is a positive probability that some progeny of the second brood will survive, particularly if egg production is not a concern. Recently, Bakker et al. (1985) have provided empirical support for this prediction by showing that some progeny of superparasitizing females can survive, at least when inter-oviposition time is short (1 to 3 hours).

Werren (1984) drew attention to two other attributes that would improve the fitness of superparasitizing females. The chances of survival of progeny from second broods would be increased if females could approximate the size of first broods and adjust their own brood size in a compensatory manner. Those females could increase their fitness further by increasing the fraction of males in second broods because of the bias toward females in first broods. Both *M. obsoletus* (Fig. 1) and *N. vitripennis* (Werren, 1984) appear, in an approximate way, to adjust the size of secondary broods. *Nasonia vitripennis* females also appear to adjust the sex ratio of second broods as predicted by the theory (Werren, 1984; but see Orzack and Parker, 1986). Possible changes in the sex allocation pattern of superparasitizing *M. obsoletus* females are being investigated.

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NOTES AND COMMENTS

THE EUROPEAN LADY BEETLE *PROPYLEA QUATUORDECIMPUNCTATA*: NEW LOCALITY RECORDS FOR NORTH AMERICA (COLEOPTERA: COCCINELLIDAE)

Propylea quatuordecimpunctata (L.), an important coccinellid predator of cereal aphids in Europe, was first collected in North America near Ste-Foy (Québec Co.), Québec in August 1968 (Chantal 1972). The beetle was collected repeatedly by Chantal at the same locality during the next four seasons, suggesting that the species was already well established when first captured. The origins of the colony are unknown, but the 1968 recovery certainly predates by two years any of the intentional (but unsuccessful) releases of this species made in Delaware, New Jersey, and Oklahoma (Gordon 1985, Rogers et al., 1972). In 1980, Larochelle and Larivière presented dates of subsequent collections of this insect in nine more counties in Québec, mostly adjacent to the St. Lawrence River: (1972) Montmorency; (1974) Champlain, Portneuf; (1976) Saint-Maurice; (1977) Ile de Montréal; (1979) Charlevoix-Est, Charlevoix-Ouest, Laprairie, and Levis. It is my purpose here to provide seven additional county records for *P. quatuordecimpunctata* which extend the known distribution of this exotic species in southern Québec and into the United States.

In 1984, personnel of the Québec Department of Agriculture (SRDC) collected specimens of *P. quatuordecimpunctata* in two more Québec counties: Deux Montagnes and Montmagny (M. O. Guibord, SRDC, Complexe Scientifique, Ste-Foy, Québec, *in litt.*). The first U.S. collections were taken by B. Parker in Vermont, in Grand Isle Co. in 1984, and in Chittenden Co. in 1985 (R. T. Bell, Dept. Zoology, Univ. Vermont, Burlington, *in litt.*).

During early June 1986, I collected this beneficial species while sweeping alfalfa, vetch, and roadside weeds in southern Québec. These collections resulted in two new county records in Québec: Rouville Co. (near St. Hilaire) and Stanstead Co. (near Massawippi), plus one new record in New York: Clinton Co. (at Plattsburgh). The identity of specimens from both New York and Vermont was confirmed by R. D. Gordon (Systematic Entomology Laboratory, USDA-ARS, Washington, D.C.).

The known distribution (Fig. 1) stretches for approximately 420 km and probably encompasses over 36,000 km². It is doubtful that the insect has dispersed much further southward than illustrated, because our recovery attempts in adjacent counties were negative during the 1986 season. Assuming that the beetle has dispersed from the 1968 find at Ste-Foy, Québec to the 1986 find at Plattsburgh, New York, one can estimate the average rate of movement during those 18 years at 16 km/year. In view of this rather slow dispersal rate, I would suggest that the beetle should be recolonized at distant sites to assist its spread.

Although the origins of the establishment in Québec are unclear, based on the distribution pattern thus far known, I tend to agree with Larochelle and Larivière (1980) who suggest the possibility of an accidental introduction of the beetle from European vessels moving along the St. Lawrence Seaway. Considering its ability to
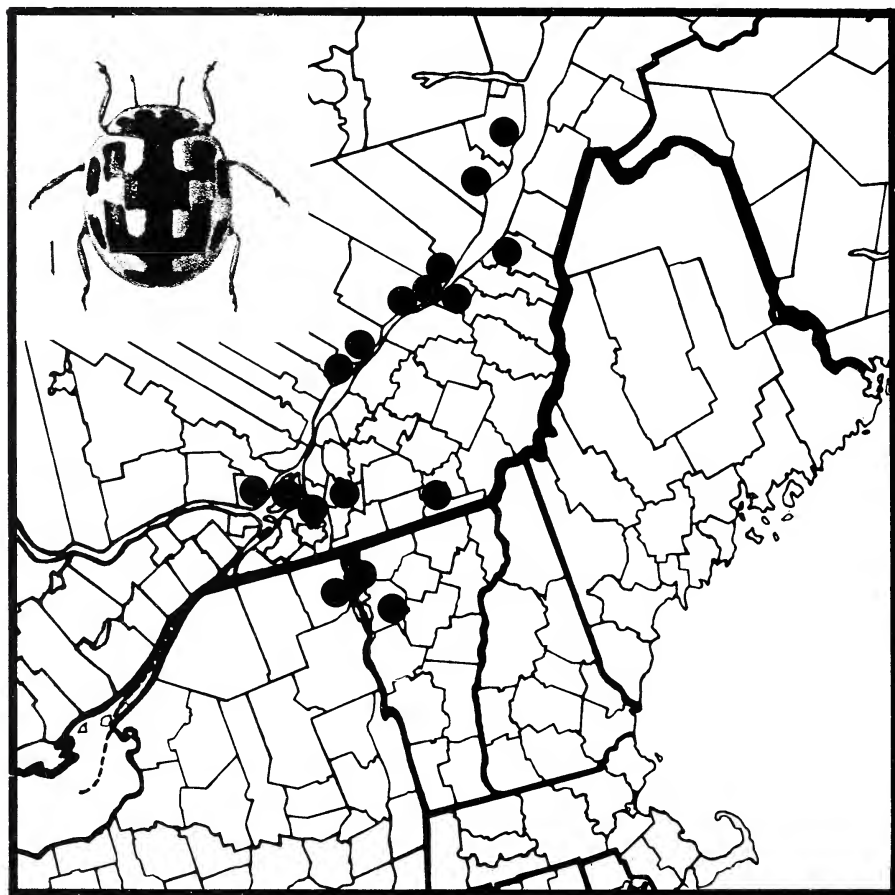
Fig. 1.   Known distribution of *Propylea quatuordecimpunctata* in North America. Habitus drawing of adult adapted from Moreton, 1969 (elytral pattern is variable).

exist over a wide area in the Palearctic region and its successful adaptation to the harsh climate of Québec, it seems likely that *P. quatuordecimpunctata* will eventually extend its range throughout much of North America.—*Richard J. Dysart, USDA-ARS, Beneficial Insects Research Laboratory, 501 S. Chapel St., Newark, Delaware 19713.*

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PREY CARRIAGE ON THE STING BY *SERICOPHORUS RELUCENS* (HYMENOPTERA: SPHECIDAE: LARRINAE)

Most species of sphecid wasps use their mandibles or legs to carry their prey as they fly back to their nests (Evans, 1962; Genise, 1980). Transporting the prey on the sting is known from only a few species in the Crabroninae (Evans, 1962; Peckham et al., 1973; Genise, 1980). I report here the carriage of prey on the sting by a member of the Larrinae, *Sericophorus relucens* F. Smith.

I observed a female of *S. relucens* catch a *Musca vetustissima* Walker from a group of bushflies circling my head, at 14:08 on 11 Dec 1985, at Camp Pincham in Warrumbungles National Park, New South Wales, Australia. The wasp, grappling with the fly, landed on the ground near my feet and stung it in the ventral part of the thorax. Through binoculars I watched as she made two short (5–15 cm) flights with the fly impaled on her sting. She then flew off and I caught her in a net where the bushfly was clearly seen to be still impaled on her sting. The fly was dislodged from the sting for the first time when they were placed in a vial. A week previously I had observed another female of *S. relucens* catch a bushfly. Her actions reminded me of *Oxybelus uniglumis* (Linnaeus), a species that transports prey on its sting, prompting me to watch closely when it happened again.

Transporting prey on the sting is unusual in the Sphecidae. The primitive and most common type of prey transport is using the mandibles (Evans, 1962; Genise, 1980). Many genera use the middle legs as the principal support for their prey, while only 3 genera use the hind legs. Two of these 3 genera, *Oxybelus* and *Sericophorus,* are those which include species that transport prey on the sting (Peckham et al., 1973; Matthews and Evans, 1970). *Sericophorus* therefore, provides another example of the evolutionary trend described by Evans (1962) of the shift of prey further back for transport.

Both *S. relucens* and the several species of *Oxybelus* that carry their prey on their sting, prey upon Diptera (Peckham and Hook, 1980). Steiner (1978, 1979) has shown in *O. uniglumis* that a single sting is directed toward the one major fused ganglionic mass of the fly. He has also shown, at least in the captive situation, that the sting is

not removed after paralysis and before transport. This appears to hold for *S. relucens*. Presumably the single sting and use of small dipterous prey have been important in the evolutionary convergence of prey carriage on the sting in these two groups of wasps. Some authors include both *Sericophorus* and *Oxybelus* in the Larrinae (Evans, 1964; Lomholdt, 1985). Despite being considered in the same subfamily, they are not closely related (Lumholdt, 1985) and therefore prey transport on the sting in these two taxa is a convergence, not a result of common descent.

The fly and wasp were identified by Dr. D. Colless (Australian National Insect Collection, Canberra) and Dr. O. Lomholdt (Zoologisk Museum, Copenhagen), respectively and are preserved at their institutions. Chris Thomson and Chris Reid provided helpful advice on the manuscript.—*David B. McCorquodale, Department of Zoology, Australian National University, GPO Box 4, Canberra, ACT, 2601, Australia.*

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OBSERVATIONS ON THE SWARMING BEHAVIOR OF *EUCHELICHIR LONGIPES* JEANNEL IN NORTHERN MADAGASCAR (HETEROPTERA: ENICOCEPHALIDAE)

Aerial swarming behavior in members of the Enicocephalidae has been reported by many authors, but little information is available on the prevailing conditions that

might influence such behavior, especially in the tropics. It was thus with some interest that I came upon several swarms of *Euchelichir longipes* Jeannel on the morning of 16 November 1986 in the Mt. d'Ambre forest reserve south of Diego Suarez, Madagascar. I observed the insects swarming in groups of 10 to 30 along the trail to the Petite Cascade, at an elevation of 990 m (3,250 ft), and took the air temperature as 24°C (75°F) in the shade. The swarms were vertically distributed, appearing as spiralling columns extending from 1 to 6 m above the ground. Similar swarms were observed by John Wenzel of the University of Kansas, who was working along the crest of a nearby ridge at least 150 m above the Petite Cascade trail. Both of us agreed that the swarms occurred in patches of sunlight within the generally dark forest and were mobile, subsiding when clouds obscured the sun and then reforming in another brightly lit spot when the sun reappeared. This swarming activity was first noticed at approximately 10:00 AM, and had mostly subsided within an hour afterwards. In three full days of work on the mountain this was the only trace we saw of these insects.

The Mt. d'Ambre reserve protects a primary evergreen montane forest, which in the vicinity of the forest station near the Petite Cascade receives a total annual rainfall of 2,600 mm and experiences a mean annual temperature of 17°C (Donque, 1972). The area had received light and intermittent showers the day before the swarming, but according to local foresters there had been little rain during the previous two weeks, although clouds frequently formed over the upper slopes of the mountain due to rising onshore trade winds. The Diego Suarez region of northern Madagascar has a pronounced seven month dry season lasting from May to mid-November, followed by a very rainy period that generally commences in the third week of November at the onset of the northerly monsoon. By mid-November of 1986 the baobabs bordering the bay at Diego Suarez were already beginning to leaf out in anticipation of this change. On Mt. d'Ambre the dry season is moderated by altitude, with rain falling on a more continuous basis throughout the year, but the general annual distribution of precipitation is similar. It thus appears that enicocephalid swarming, and presumably mating, is timed to occur at or immediately prior to the beginning of the heavy rains in this region.—*Dan A. Polhemus, Univ. of Colorado Museum, 3115 S. York St., Englewood, Colorado 80110.*

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BOOK REVIEWS

Manual of Neartic Diptera, Volume 2.—J. F. McAlpine (ed.) 1987. Research Branch Agriculture Canada Monograph 28, Minister of Supply and Services, Quebec. Pages 675–1332. $68.35 U.S.

The companion volume to the first part of Manual of Nearctic Diptera (McAlpine et al., 1981) is here. It covers, in a chapter devoted to each, 64 families, from the primitive ("Aschiza") Muscomorpha all the way to the Pupipara, and in a manner equally superb to volume one. There is also in the volume three and one-half pages of corrections and addenda to volume one. Given the amount of detail in each volume, were some minor mistakes not made, it would be a great surprise. The upcoming volume three will contain the last three chapters, on phylogenies of the Nematocera, orthorrhaphous Brachycera, and the Muscomorpha, as well as a composite index for both volumes.

As in volume one the amount of wonderful illustrations is astounding: to my count, 1,817 drawings in volume two! They are primarily of habitus, head, wing, and terminalia, and were done in the same style throughout the entire manual (at least 3,000 drawings total) because all but several dozen illustrations were done by one person, Ralph Idema. Some of the drawings were used in taxonomic papers published by the Ottawa group ever since 1965, which is around the time Mr. Idema began work there, and when inspiration for the Manual had already jelled. The achievements of this artist are a model as to what all revisionary taxonomists wish to produce, and the drawings will be a lasting contribution to Diptera taxonomy for their detail and clarity, as well as style. Students should find the Manual as a reference for technique in pen and ink and in composition. Some notes to inspired illustrators: the outlines add depth because the line thickness was varied using a crow quill pen (this was also done for setae, and it takes considerable practice to master), the beautifully-graded stippling was done using a rapidograph with a point finer than that used for some outlines, and the "halo" around overlapping lines, such as at the edge of a seta, was produced by scratching away the surface of the drawing film. Despite a lesson in technique several years ago, I have yet to achieve Idema's effect in rendering the eyes. Mr. Idema: for the sake of insect taxonomists, please draw a small handbook on illustration techniques.

Most of the chapters were written by the current and active taxonomist on the family, and as a result, references up to 1986 are included in some chapters. However, just how recent is the literature review varies considerably with the chapter.

The accounts of each family, 107 in all, include sections on the adult, immature stages (where known), biology and behavior (such as breeding sites, many records of which were previously unpublished), and a section on classification and distribution under which there are usually comments regarding the known fossils. The chapters on the larger families which have not been comprehensively treated in a single work are a major taxonomic contribution of the Manual. Previously, keying Tipulidae, Empididae, Dolichopodidae, Mycetophilidae, Lauxaniidae, Chloropidae, and many Muscoidea to genus was a nightmare for the non-specialist. The only negative comment of mine concerns the very long and detailed descriptions of each tagma of the

adult at the beginning of each chapter, which should have been shortened into a more diagnostic format.

Because much material remains yet unprepared and unstudied from most amber deposits, comments on fossils are anecdotal. All the major amber deposits—the Lower Cretaceous of Lebanon (Schlee and Dietrich, 1970), Lower Miocene—Upper Oligocene of Chiapas, Mexico and the Dominican Republic (Hurd et al., 1962; Baroni-Urbani and Saunders, 1982), and the Upper Cretaceous of Canada (McAlpine and Martin, 1969)—are more unworked than studied. For example, in the Dominican amber collection at the AMNH are specimens representing very interesting records of Anisopodidae, several genera of Phoridae, Micropezidae, Clusiidae, Odiniidae (*Odinia*), Anthomyzidae, Aulacigastridae (3 genera), Asteiidae (*Asteia*), Milichiidae (various genera), Lanxaniidae, Chloropidae (3 genera), Drosophilidae (Grimaldi, 1987), and the first records of at least Ephydridae (*Beckeriella*), among many other families. Meunier described a great deal of Baltic amber Diptera, as did Hennig later on, but unlike the latter, Meunier had a great propensity for proposing new genera simply on paleontological grounds. Many Meunier taxa will need to be re-examined before those names will be phylogenetically meaningful.

A few nomenclatural proposals and changes are buried in the text. The genera *Neossos* and *Paraneossos,* formerly placed in the Trixoscelididae, have been put into the Heleomyzidae. As had been discussed, there is good evidence for probably synonymizing the trixoscelidids with the Heleomyzidae, but the remaining genera are left in the Trixoscelididae as is best for a work of this type. I spotted two new taxa: *Acantholespesia* for the Tachinidae (for which couplet 47′ is the diagnosis), and the subfamily Epiplateinae for the Richardiidae, (containing *Automola, Epiplatea,* and the unusual genus *Omomyia*). At least for the latter instance, it would be preferable to have new names for higher taxa proposed in the context of a major revisionary paper. I believe that it will soon be published that *Sphyracephala brevicornis* (Say) isn't the only North American dropsid: *S. subbifasciata* Fitch is sympatric with, but distinct in color pattern and male genitalia from, *S. brevicornis.* The two species were synonymized for over 80 years.

Contributions from one prominent North American dipterist for the Manual are entirely absent save for at least the repeated reference to a large study of his (Griffiths, 1972). One might surmise by reading just the critiques of the Manual (Griffiths, 1981) that volume one was about 400 pages worth of male terminalia homologies, and of the interordinal homology of the "paramere" and epandrium in particular. Any lack of cooperation between these Canadian parties is unfortunate for Griffiths' knowledge of particular North American taxa could have been used for valuable contributions in the Manual. McAlpine agrees with some of the hypotheses proposed in the 1972 study by Griffiths, such as the sister-group relationship of the Chryomyidae and the Sphaeroceridae. But there is not always agreement between the two; for example, despite evidence which corroborates Griffiths' hypothesis that at least *Campicheota* should be separated into a family in the Drosophiloidea (Chandler, 1987), it is kept in the Diastatidae by McAlpine. Differences are summarized best in the classifications presented in Griffiths (1972) and in the beginning of volume one of the Manual. The Manual adheres to a conservative classification, such as use of the paraphyletic Nematocera, orthorrhaphous Brachycera, and Aschiza Muscomorpha, which I suppose were used mostly for convenience at the time. Use of Griffiths' (1972) highly

hierarchical, genealogical classification was perhaps seen to be too cumbersome for a reference book like the Manual, as well as probably incorrect in places, but that classification is used in the "Flies of the Nearctic Region" (which Griffiths edits). The two works, hardly mutually exclusive, are fascinating in their dichotomy: the meticulous and comprehensive treatment of the Manual, and the very original and synthetic, in places cavalier, treatment of Griffiths (1972). The two works serve different uses: that of the Manual's first two volumes is almost entirely for identification and is not revisionary, so it should prove interesting to see how the results of volume three mesh with Griffiths' 1972 book.

Basically the Manual is a technical masterpiece. Volumes one and two are not a truly scholarly work, but are as encyclopedic as is possible for a work of this size. Regardless of the type of entomologist that you are, this book is a must.—*David Grimaldi, Entomology Department, American Museum of Natural History, New York, New York 10024.*

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MAKING THE GRADE: A CLASSIFICATION OF SOME NORTH AMERICAN CARABIDAE

Cladistic Analysis of North American Platynini and Revision of the *Agonum extensicolle* Group (Colleoptera: Carabidae).—James K. Liebherr, 1986 University of California Publications in Entomology (Volume 106). x + 198 pp. $16.95 (paper).

This work is a systematic revision of a group of North American ground beetles belonging to the tribe Platynini. The contents are divided into sections that are more or less standard for a modern systematic revision. Initial sections provide introductory background information, a cladistic analysis of selected North American platynine species, and keys to the genera of this tribe and to the species of *Agonum* in

North America. The remainder of the work treats a group of seven species, the *Agonum extensicolle* species group. Included are: circumscription of species, analysis of dispersal capabilities, taxonomic treatment, phylogeny, biogeography, and appendices. The work is divided logically into sections, but only those of general interest to a broad entomological audience will be discussed here. My criticisms of this work are largely based upon a different philosophical approach to classification and do not detract from the high quality, detailed taxonomic treatment that Liebherr presents.

The section treating relationships of North American Platynini underscores the difficulty of deriving a meaningful classification from an analysis using the exemplar approach and restricting the included taxa to a particular region. Slightly more than half of the 56 characters used were genitalic or of the female reproductive tract. The 43 exemplar taxa used for the phylogenetic analysis represent less than a quarter of the North American Platynini fauna. This analysis is useful for understanding the placement of the *Agonum extensicolle* species group and finding appropriate outgroup taxa. Liebherr purports to derive his classification, as listed in his Appendix 2, from this preliminary cladistic analysis. Yet his scheme is quite different. Unnatural groups include: *Platynus* which is paraphyletic; *Agonum,* which Liebherr readily admits, is polyphyletic; and only four of nine species groups of *Agonum* are depicted as monophyletic. One of these, the *Agonum quadrimaculatum* species group is monotypic.

The bulk of this work is the taxonomic treatment of the *Agonum extensicolle* species group, with subsequent discussions of its phylogenetic and biogeograhic history. Seven species are recognized; two of these are new. An indication of the taxonomic difficulty of this group of beetles is the number of names proposed for species in this group. There are 26 synonyms for the five previously recognized species, and 14 of these synonymies are new. Liebherr uses qualitative morphological, electrophoretic, and biometric data for the basis of his species concept, and he explicitly states his criteria for recognizing species as distinct lineages; this part of his work is excellent. For example, there are 16 synonyms for *Agonum decorum,* which is polymorphic for color and setation. Both of these characteristics are often used to discriminate between closely related species of Carabidae. Here, a proper understanding of the heterogeneity and intraspecific variability of *A. decorum* is clarified by biometric and electrophoretric analyses of populations. These data are not as useful, however, for determining phylogenetic relationships within the *extensicolle* species group grade.

In the section treating the phylogeny of these species, my methodological and philosophical objections are similar to those for the Platynini analysis discussed earlier. The *extensicolle* group is never supported as monophyletic, although it would be if expanded to include *Agonum quadrimaculatum.* Liebherr states in the introduction that this "group is distinct within the genus, supporting recognition of it as a monophyletic group." Distinctiveness is an inappropriate measure of monophyly; common ancestry is the only relevant criterion for forming natural groups.

Liebherr presents detailed accounts of the present distributions of these species, and he interprets historical events which may have contributed to these distributions. He also compares these with similar distributions in other organisms. This historical biogeographic analysis is thorough and useful for other workers interested in North American biogeography. His analysis is based upon two trees. The first tree, derived from qualitative morphologiccal data, is strictly dichotomous, while the second tree, a consensus tree, has a basal trichotomy. The historical implications for each of these phylogenies is discussed. It is unfortunate that *A. quadrimaculatum* was not included

so that these interpretations could be based upon an analysis of a monophyletic group.

The most interesting aspect of the proposed biogeographic history of these beetles are the postulated speciation events, suggesting rapid evolution and speciation during the Pleistocene. For example, he suggests that speciation between *A. extimum* and *A. parextimum* occurred one, or at most, two million years ago; and he suggests that *A. decorum,* presently widespread in North America, and *A. elongatulum,* presently restricted to peninsular Florida, separated about 160,000 years ago. This latter event, associated with higher sea levels, is correlated with available data for sea levels during the Sangomon Interglaciation. Yet recent studies (Coope, 1978, 1979; Matthews, 1977, 1979) suggest that there was little morphological change and no documented case of Pleistocene speciation in North American or European Coleoptera. Matthews (1979) reported several species of *Agonum,* possibly conspecific with extant species, from the Beaufort Formation in Alaska. These fossils, from the Miocene, are at least eight million years old. These species are not included in the exemplar Platynini analysis. If these species were included, where would they be located on the tree? Why are apparent rates of speciation so much faster in the *extensicolle* group? Maybe they aren't. Liebherr uses Nei's genetic distance to set an electrophoretic clock to estimate probable dates of divergence between species. Acquiring similar data for extant species, and their relatives, represented by Miocene fossils may provide an internal check for possible dates of divergence within *Agonum* and contribute to an understanding of the problem of species constancy in the Pleistocene.—*James Pakaluk, Department of Entomology, University of Kansas, Lawrence, Kansas 66045.*

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Mailed April 28, 1988

TWO NEW *SCAPHINOTUS* FROM ARKANSAS WITH NOTES ON OTHER ARKANSAS SPECIES (COLEOPTERA: CARABIDAE: CYCHRINI)[1,2]

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Abstract. —Two new ground beetles species in the tribe Cychrini are described from western Arkansas: *Scaphinotus* (s. str.) *parisiana* and *Scaphinotus* (*Nomaretus*) *infletus*. Distribution records within Arkansas are given for four additional cychrine species. A cladogram of relationships for the five known species in the subgenus *Nomaretus* is proposed.

A number of papers on the ground beetle tribe Cychrini, as it occurs in North America, have been published including the following: Valentine, 1935; Van Dyke, 1938; Bell, 1959; Ball, 1960, 1966; Gidaspow, 1973. These papers provide a working idea of the systematics and distribution of the cychrine fauna in North America: *Sphaeroderus* Dejean (6 species); *Cychrus* Fabricius (3 species); *Scaphinotus* Latreille (7 subgenera, 46 species).

There are two large cychrine faunas, one eastern and one western. One species, *Scaphinotus elevatus* (Fab.) ranges from the eastern to the western United States. Cychrines inhabiting the mid-continent, the Ozark-Ouachita highlands, have affinities with both the eastern and western fauna. Many cychrine species appear to be endemic to specific mountain tops or at least to specific mountain ranges. There is also a lowland fauna consisting of a number of distinct species in several subgenera in *Scaphinotus*.

In eastern North America there are a number of geographical areas that are important because of the endemic species that occur in specific habitats in these areas, e.g., the southern Appalachians (various papers in Holt, 1969), peninsular Florida (Howden, 1963), and the Ozark and Ouachita mountains, Robison and Smith (1982), to mention a few. The Ozark-Ouachita mountain uplift area of western Arkansas has yielded a significant number of new species in several insect groups, including the Trichoptera, Plecoptera, and Coleoptera (Robison and Smith, 1982). The new species described in this paper are presently known to occur only in western Arkansas.

The new species of *Scaphinotus* s. str. described in this paper seems to have its closest affinities with the previously described *S. unicolor* (Fab.). *Scaphinotus unicolor* along with *S. elevatus* was set apart from other *Scaphinotus* species in a key given by Van Dyke (1938). Van Dyke characterized these two species in couplet 5 of his key as follows: "Pronotum either dull and finely or coarsely rugose, not distinctly

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punctured, or smooth with coarse punctures limited to depression, reflexed side margins wide throughout; elytra with continuous and sharply defined striae and intervals, the strial punctures close together, the lateral margin at humeri very broadly reflexed, epipleura densely punctured and rugose; fourth antennal segment glabrous like preceding segments; male front tarsi less broad, segments never broader than long."

Using Van Dyke's key, the new *Scaphinotus* species described here would fall into the *unicolor-elevatus* couplet.

The classification and ancestral relationships of *Scaphinotus elevatus, S. unicolor,* and the two other eastern species in this subgenus, *S. viduus* (Dej.), *S. webbi* Bell, have been discussed by Bell (1959) and Ball (1966). When Bell described *S. webbi,* his comments pointed out many of the problems relevant to establishing clear relationships among the species. Bell noted that *S. webbi,* "combines the widely reflected prothoracic margins of *Scaphinotus* s. str. with the two pairs of marginal setae of the subgenus *Irichroa."* *Irichroa* had been used as the subgenus of *S. viduus.* Thus the characters that had been used to separate the two subgenera *Scaphinotus* and *Irichroa* could no longer be used. Accordingly, *Irichroa* became a synonym of *Scaphinotus.* Bell also noted that the mixture of characters, external and aedeagal, shared by the different eastern species of *Scaphinotus* made it difficult to determine phylogenetic relationships.

Ball (1966), in his treatment of the western *Scaphinotus petersi* group, relegated the four eastern species of *Scaphinotus* to four different and distinct groups. Ball said "Bell (1959) implied that the four eastern species are phylogenetically about equidistant from one another. The classification presented here is consistent with this implication." We have also noted the characters mentioned by Bell and Ball and are also unable to suggest a cladistic (phylogenetic) interpretation. We defer proposing a cladogram of *Scaphinotus* relationships and will only add a new species to Ball's *unicolor* group.

The new *Nomaretus* being described in this paper, its characters, as well as the characters of previously described species, do indicate reliable cladistic relationships. These characters are discussed in detail in a subsequent section.

<div align="center">

Scaphinotus (s. str.) **parisiana**, new species

Figs. 1, 2, 3

</div>

Holotype. ♂. Arkansas, Logan Co. 13 mi southwest of Paris, Northwest slope of Magazine Mountain, 26 June 1985. Robert T. Allen, Boyd Matthews, Andrew Wilbers, David Jackson, collectors (UAIC), 1♂ (George Ball, Univ. Alberta), 1♂ (American Museum Natural History), 1♂ (British Museum, Natural History).

Etymology. This species is named after the city of Paris, Arkansas, located at the base of Magazine Mountain where the species was first collected by the senior author.

Description. COLOR. Dorsal. Head: black. Pronotum: black to dark purple. Elytra: dark purple. Ventral. Entire surface: dull black. HEAD. Dorsal. Labrum: 4 (sometimes 3) setae in notch, 1 seta (each side) apically. Fronto-clypeal suture: distinct. Posterior: constricted behind the eyes. Supra-orbital setigerous punctures: 1 pair. Surface: microsculpture present or not, when present weak, isodiametric; impunctate. Ventral. Mentum: microsculpture, distinct, isodiametric; lateral lobes, broadly round-
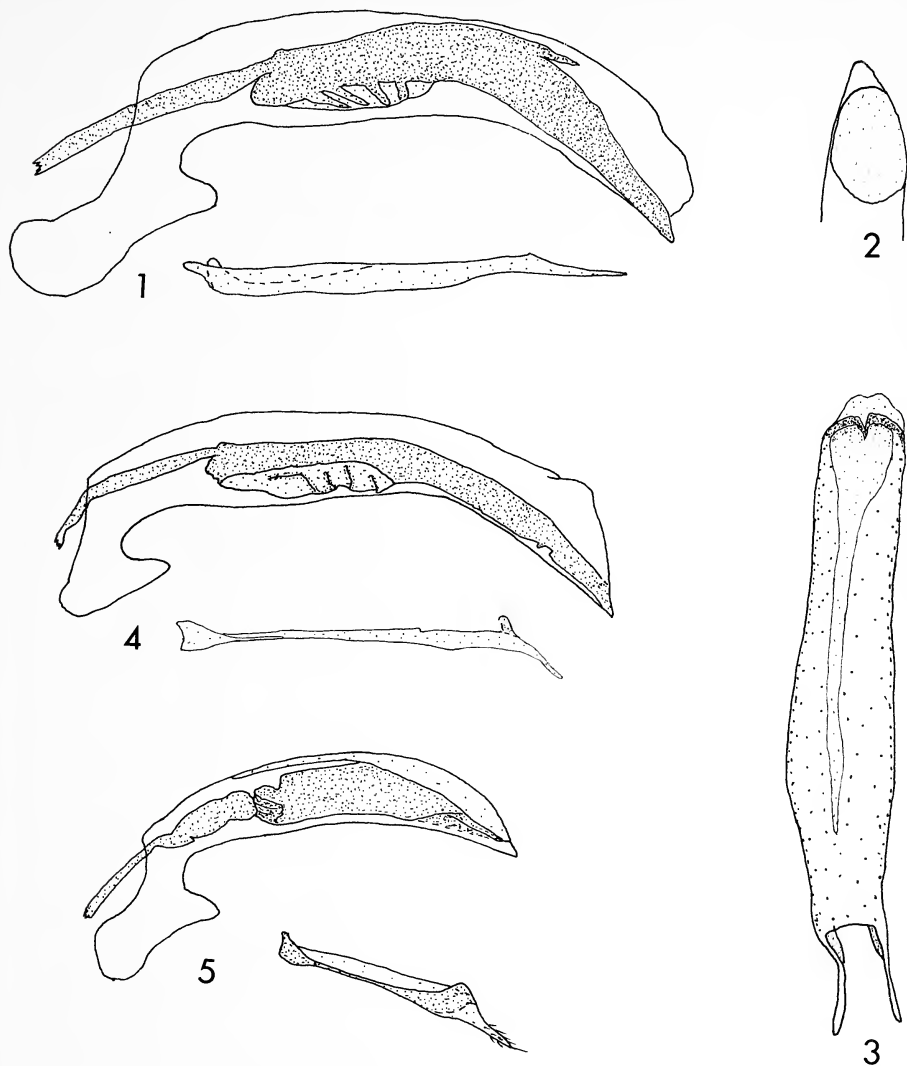
Figs. 1–5. Male aedeagi. Figs. 1–3. *Scaphinotus parisiana*: 1. Right lateral. 2. Dorsal, apex. 3. Dorsal. Fig. 4. *Scaphinotus unicolor,* right lateral. Fig. 5. *Scaphinotus elevatus,* right lateral.

ed apically, distinctly margined anteriorly, less distinct laterally; tooth absent. Gular sutures: distinct. Palpi: as for the genus. Antennae: I–IV glabrous except for fixed setae; I unisetose, basal socket ball with distinct setae; II, asetose; III–IV, with scattered setae along the segment and a ring of apical setae; V–XI, pubescent. THORAX. Dorsal. Pronotum: microsculpture, where present, isodiametric; lateral margins distinctly and broadly reflexed; edge of lateral margins smooth their entire length, asetose. Surface: rugose and coarsely punctate except for small central discal area.

Median sulcus: distinct, other sulci absent. Ventral. Microsculpture: present, isodiametric. Prosternum: intercoxal process weakly margined apically; sparsely punctate near sternal-pleural margin. Proepisternum: sparsely punctate near episternal-epimeral suture. Proepimeron: sparsely punctate. Mesosternum: distinctly convex anteriorly, punctate, setose, with a median keel; posterior area distinctly margined laterally. Mesepimeron: punctate, rugose. Metasternum: punctate laterally. Metepisternum: punctate. Metepimeron: indistinct. ELYTRA. Microsculpture: absent on interval, weak in stria. Striae: distinct, 14–17, longitudinally confused laterally, distinctly punctate. Disk: asetose. Lateral margins: narrowly reflexed. Epipleura: coarsely punctate. Humeri: rounded. ABDOMEN. Microsculpture: present, isodiametric. Segments: I, coarsely punctate; II–III, punctate and rugose laterally; IV–VI, rugose laterally. LEGS. Protarsi: I–III, ventral pad present (I, apical ¼ only). Measurements. Length: 25–28 mm. Width: greatest width across elytra, 12–14 mm. AEDEAGUS (Figs. 1–3). Median lobe: cylindrical, basal lobes ⅓ length of median lobe. Parameres: elongate, distinctly narrowed distally, asetose. Internal sac: within median lobe extending posteriorly ¾ length of the median lobe, with ventral folds; median ejaculatory duct narrow at attachment with the internal sac; everted internal sac covered with small scales but no distinct spines or scale groups.

Comments. Scaphinotus parisiana is very similar to, and is apparently closely related to *S. unicolor.* The principle diagnostic character for *S. parisiana* is the greatly enlarged basal lobes of the median lobe. Specimens of *S. unicolor* were collected in the immediate vicinity of *S. parisiana,* and no specimens have been found that might be considered intermediates between the two aedeagal forms. This suggests that specimens referred to *S. parisiana* are in fact a valid new species, not one end of a range of variation.

Scaphinotus (s. str.) *unicolor* Fabricius
Fig. 4

Two specimens have been collected in Arkansas: Logan Co., near Paris, Magazine Mountain, 26 June 1985; Washington Co., pitfall trap, 1962.

Scaphinotus (s. str.) *elevatus* Fabricius
Fig. 5

Scaphinotus elevatus seems to be the most common cychrine species in Arkansas. Collecting records include the following: Benton Co., Bentonville, Osage (one specimen each); Boone Co. (one specimen); Craighead Co. (one specimen); Searcy Co. (one specimen); Washington Co. (34 specimens). Specimens have been taken in all months from April through November.

Scaphinotus (Nomaretus) infletus, new species
Figs. 6–10

Holotype. ♂. Arkansas, Newton Co., Alum Cove Scenic Area, 20 June 1974 (UAIC). Robert G. Chenowith collector.

Paratypes. 2♂♂ (UAIC), Newton Co., 5.9 mi S. Mt. Judea, Pitfall trap, 11 July 1974, colls. J. Heiss, R. Chenowith, R. Howard; Newton Co., Lost Valley State Park, 17 May 1973, coll. R. G. Thompson.
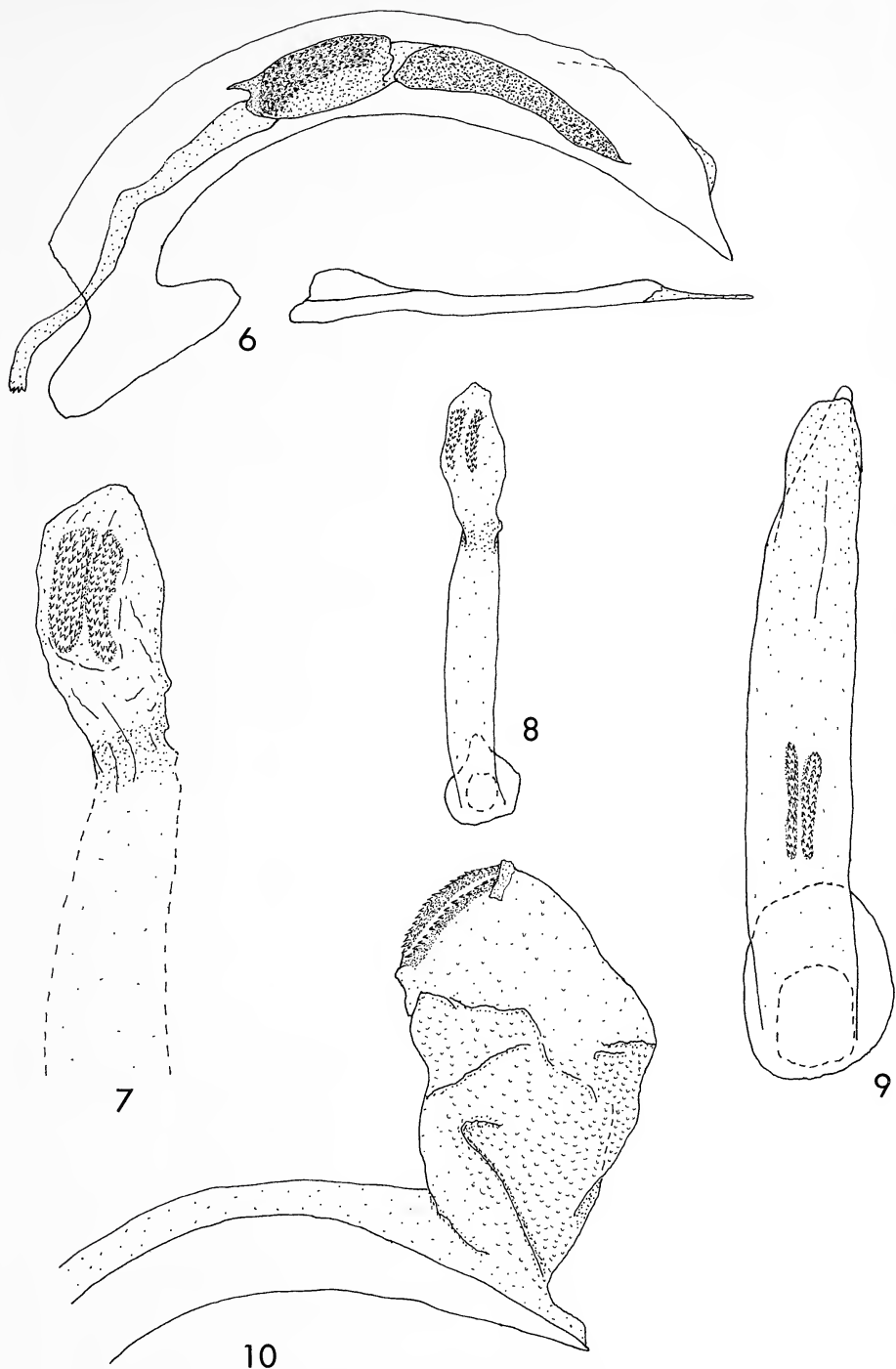
Figs. 6–10. Male aedeagi, *Scaphinotus* (*Nomaretus*) *infletus*: 6. Right lateral. 7. Dorsal, internal sac everted, enlarged. 8. Dorsal, internal sac everted distally, median lobe basally. 9. Dorsal, internal sac not everted. 10. Right lateral, internal sac everted.
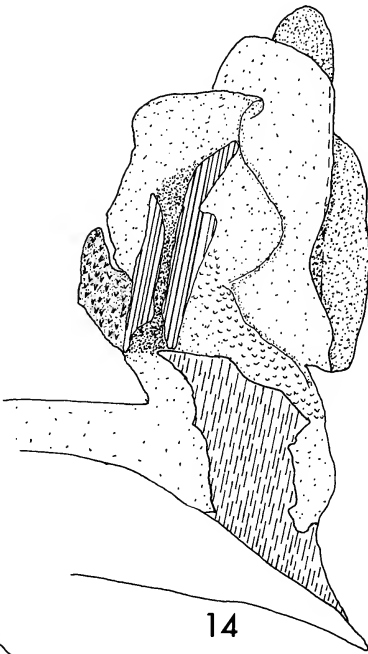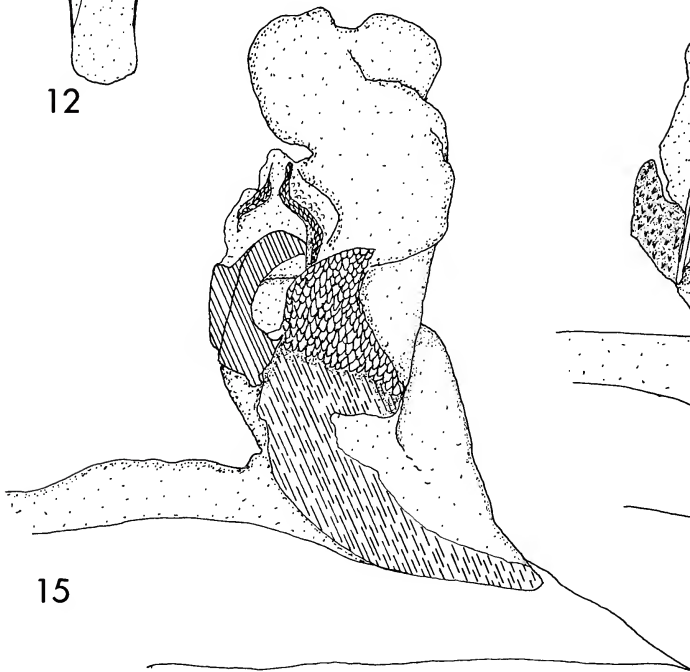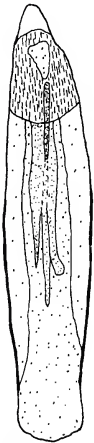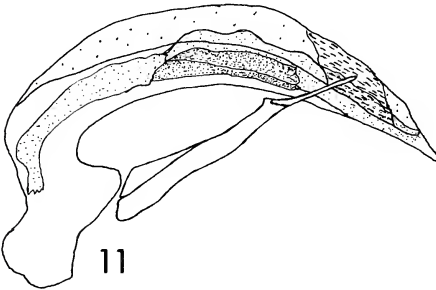
Etymology. The specific name *infletus* means "the forgotten one."

Description. COLOR. Dorsal. Head, thorax: black. Elytra: black sometimes with a purple tint. Ventral. Entire surface black, sometimes shining. HEAD. Dorsal. Labrum: 4 setae at the base of the notch, 1 seta (each side) apically. Fronto-clypeal suture: distinct. Posterior: constricted behind the eyes. Supra-orbital setigerous punctures: 1 pair. Surface: impunctate; microsculpture distinct, isodiametric laterally, elongate medially. Ventral. Mentum: microsculpture distinct, isodiametric; lateral lobes rounded, not margined laterally; tooth absent. Gular sutures: distinct. Palpi: as for the genus. Antennae: I, unisetose; II, with a ring of setae; III–XI, pubescent. THORAX. Dorsal. Pronotum: microsculpture distinct, isodiametric; lateral margins narrowly reflexed, widest in front of middle. Surface: disk, smooth; coarsely punctate area anteriorly (set off by the anterior marginal sulcus) and posteriorly (between the weakly defined basal fovae). Ventral. Prosternum: microsculpture, distinct, isodiametric; intercoxal process weakly margined at apex; coarsely punctate anteriorly and laterally. Proepisternum: microsculpture, distinct, isodiametric; coarse punctures only along sternal-episternal suture. Proepimeron: microsculpture absent, shining; coarsely punctate. Mesosternum: microsculpture present laterally and posteriorly, elongate; coarsely punctate; each side of the anterior median keel declivous; posterior area deeply margined laterally. Mesepisternum: microsculpture, weak if present, shining; sparsely, coarsely punctate. Mesepimeron: microsculpture absent; sparsely, coarsely punctate. Metasternum: anterior margin deeply emarginate; microsculpture present, elongate; coarsely punctate laterally. Metepisternum: microsculpture weak or absent; coarsely punctured. Metepimeron: indistinct. ELYTRA. Microsculpture: distinct on intervals, elongate. Striae: 10 distinct, deeply punctate striae. Disk: asetose. Lateral margins: narrowly reflexed. Epiplura: coarsely and densely punctate. ABDOMEN. Microsculpture: distinct, isodiametric or elongate. Segments: I, coarsely punctate; II–V, coarsely punctate laterally; VI with a few coarse punctures in anterior-lateral angle; IV–VI, with a distinct, deep sulcus just behind each anterior margin. LEGS. Protarsi of males: I, ¾ of ventral surface with squamous setae; II–III, ventral surface with squamous setae. Measurements. Length: 9–10 mm. Width: greatest width across elytra, 4–5 mm. AEDEAGUS (Figs. 6–10). Median lobe: cylindrical, basal lobes ¼ the length of the median lobe. Parameres: elongate, distinctly narrowed distally, asetose. Internal sac: two elongate, parallel scale groups present on dorsal surface (visible through the wall of the median lobe), additional scales and sclerites absent.

Comments. Scaphinotus (*Nomaretus*) *infletus* is similar to *S.* (*Nomaretus*) *fissicollis* in external appearance. The distinct scale groups on the internal sac of the aedeagus of *S. infletus* readily separate it from all other species in the subgenus. The squamous setae on the ventral surface of the first protarsal segment of the males also appears to be a reliable diagnostic character. In *infletus* the setae cover at least ¾ of the ventral surface of the tarsomere, whereas in other species of the genus ½ or less of the ventral surface is covered by these setae.

←

Figs. 11–15.   Male aedeagi. Figs. 11–14. *Scaphinotus* (*Nomaretus*) *fissicolis*: 11. Right lateral, internal sac not everted. 12. Dorsal, internal sac not everted. 13. Right lateral, internal sac everted. 14. Right lateral, internal sac everted and slightly turned so that the two distinct sclerited are apparent. Fig. 15. *Scaphinotus* (*Nomaretus*) *cavicollis,* right lateral, internal sac everted.

Scaphinotus (*Nomaretus*) *fissicollis* LeConte
Figs. 11–14

Gidaspow (1973) noted in her key to the species of *Nomaretus* that *fissicollis* "usually" has only two lateral pronotal setae. At least one-half of the Arkansas specimens we have examined have three or more setae along the lateral margins. Gidaspow also illustrated the extent of the squamous setae covering the ventral surface of the male protarsal segments of *fissicollis* and *bilobus* Say. The ventral surface of the protarsal segments in males of *fissicollis* more closely resembles the illustrations of *bilobus* than those of *fissicollis* as given by Gidaspow. Utilizing only the pronotal setae and the extent of coverage of the protarsal squamous setae might lead to confusion of Arkansas *fissicollis* and the species *bilobus*. But the aedeagi of the two species are distinctly different. We mention this set of circumstances because *bilobus* has been collected in extreme southern Missouri (Gidaspow, 1973) and may eventually be found in northern Arkansas.

A number of *fissicollis* specimens are deposited in the UAIC, including the following localities: Benton Co. (1 specimen); Franklin Co. (3 specimens); Fulton Co. (1 specimen); Madison Co. (1 specimen); Newton Co. (3 specimens); Stone Co. (2 specimens); Washington Co. (8 specimens).

Scaphinotus (*Nomaretus*) *cavicollis* LeConte
Fig. 15

The coarsely setate pronotum serves to readily identify this species, which is represented by eight specimens in the UAIC. The specimens are from the following localities: Crawford Co. (1 specimen); Polk Co. (1 specimen); Washington Co. (6 specimens). It has been collected in the months of June, September, October and December.

CLADISTIC RELATIONSHIPS IN THE SUBGENUS *NOMARETUS*

Gidaspow (1973) has presented the basic taxonomy of the subgenus *Nomaretus*. The present discussion of cladistic relationships is based on her work and the examination of the three *Nomaretus* species occurring in Arkansas. Plesiomorphic and apomorphic character states were established by outgroup comparison with other taxa in the tribe Cychrini.

Three sets of characters were used in establishing cladistic relationships in *Nomaretus*.

1. Squamous setae on the ventral surface of protarsal segment one of the males. Reductions in the surface covered by these setae is considered an apomorphic state.

2. The number of pronotal setae. Increases in the number of pronotal setae from the plesiomorphic state of two are considered apomorphic.

3. The presence or absence of scale groups and/or sclerites on the internal sac of the aedeagus. An internal sac with no organized scale groups or sclerites would be the plesiomorphic condition. The presence of organized scale groups and/or patterns or the presence of sclerites are considered apomorphic states.

The cladistic relationships among the five known species of *Nomaretus* are depicted in Figure 16. This cladogram represents the most parsimonius interpretation of the three characters given above.
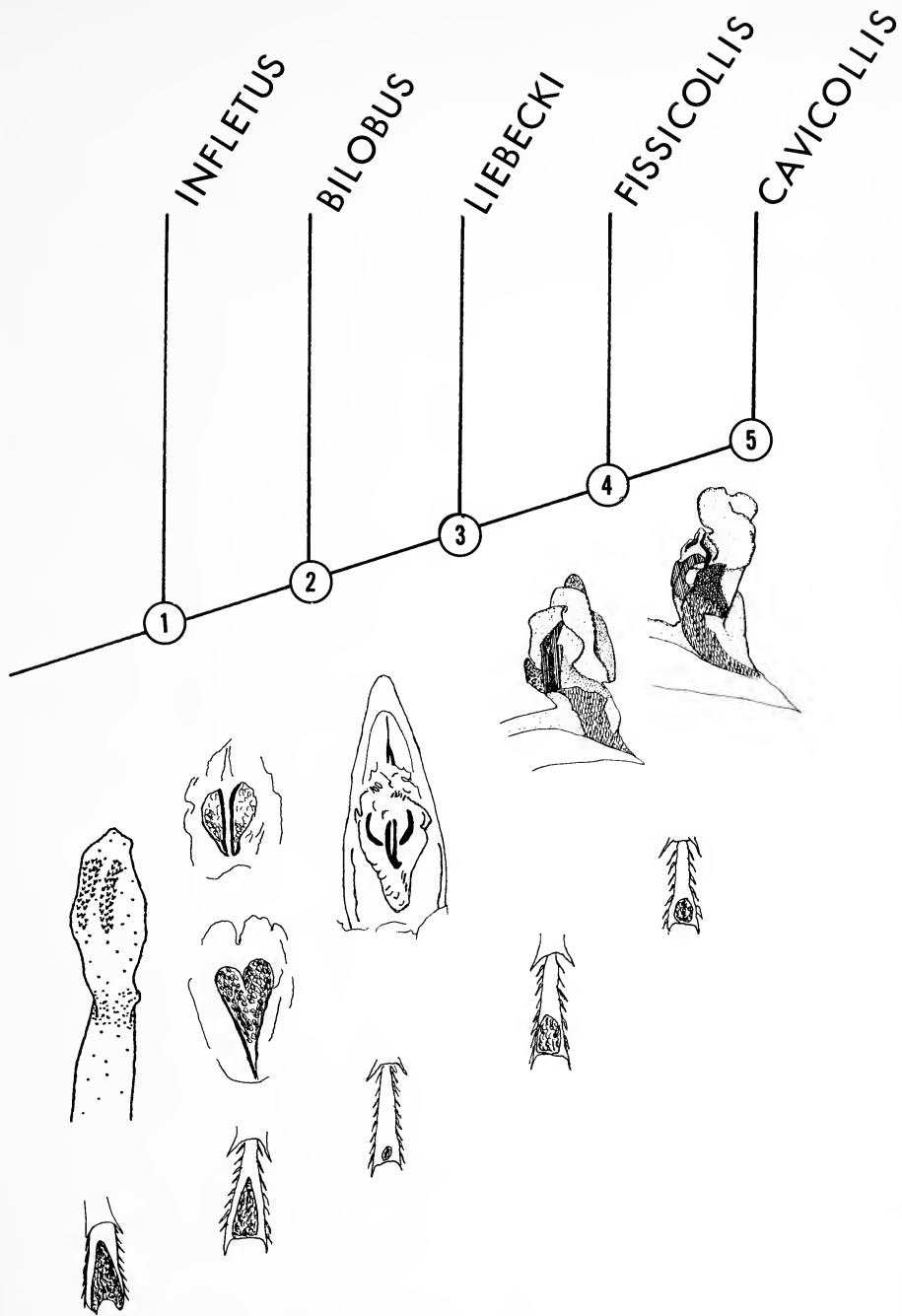
Fig. 16. A proposed cladogram of relationships among the five species in the subgenus *Nomaretus*. The top line of illustrations below the cladogram depicts changes in the armament on the internal sac of the male aedeagus. The bottom line of illustrations depicts changes in the squamous pads on the ventral surface of the male protarsi. See text for further discussion.

Scaphinotus (*Nomaretus*) *infletus* appears to be close to the ancestor that gave rise to the *Nomaretus* lineage. The internal sac of *infletus* is devoid of any sclerites but does have two distinct elongate parallel scale groups. The pronotum has only two or three setae along each lateral margin. The ventral surface of the male protarsal segment one is almost entirely covered by squamous setae.

In the lineage arising from node 1 of the cladogram, the squamae became reduced on the ventral surface or protarsal segment I of the males. This apomorphic character is shared in one state or another by four species in *Nomaretus*. *Scaphinotus* (*Nomaretus*) *bilobus* represents the next stage in the evolution of the *Nomaretus* group. The protarsal squamae are reduced in the males. The internal sac of the aedeagus possesses a peculiar structure on the surface that is not quite a distinct sclerite nor a distinct scale group. The lateral margins of the pronotum are beset with more than two pair of setae.

The next apomorphic changes to occur were a continued reduction in the squamae on the male protarsal segments (in two species, *liebecki* Van Dyke and *cavicollis*) and the development of distinct sclerotized structures on the surface of the internal sac of the aedeagus. *Scaphinotus* (*Nomaretus*) *liebecki* appears to represent the first step in the development of the aedeagal sclerotized structures. These sclerotized structures apparently became larger and more robust in *fissicollis* and subsequently fused into one structure in *cavicollis*. The anterior portion of the pronotum in *cavicollis* is beset with numerous setiferous punctures in addition to the numerous setae along the lateral margins.

At present no proposals can be offered regarding the historical events that gave rise to the isolation and subsequent speciation in *Nomaretus* populations. Four species of *Nomaretus* have overlapping ranges in the Ozark uplift area: *fissicollis, cavicollis, bilobus* and *infletus*. The fifth species, *liebecki*, occurs only a short distance south (Louisiana, Texas) of *cavicollis* populations in the Ouachita mountain uplift area. Perhaps the subgenus *Nomaretus* represents a taxonomic group whose evolution will eventually be closely associated with the geological history of the Ozark and Ouachita mountains.

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THE PHYLOGENETIC SYSTEM OF THE STENOGASTRINAE (HYMENOPTERA: VESPIDAE)

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Abstract.—The phylogenetic relationships of the genera of Stenogastrinae are investigated using cladistic methods. The cladogram here proposed is: *Liostenogaster* + ((*Eustenogaster* + *Stenogaster*) + (*Anischnogaster* + (*Metischnogaster* + (*Holischnogaster* + *Parischnogaster*)))). *Holischnogaster* is newly synonymized with *Parischnogaster*.

The Stenogastrinae, members of which might be called hover wasps, is a group of great current interest. They are thought to exhibit considerable diversity in social behavior, ranging from species which have been termed solitary (e.g., Williams, 1919), to primitively social species (lacking reproductive castes; cf. West-Eberhard, 1978), to eusocial species (Yoshikawa et al., 1969; Hansell et al., 1982; Turillazzi and Pardi, 1982). Additionally, they occupy a phylogenetically intermediate position between the solitary Eumeninae and the eusocial Polistinae and Vespinae (Carpenter, 1981). The group is thus of particular importance in the study of the evolution of social behavior in wasps. Reflecting this, the past decade has seen more behavioral studies on this subfamily than any time previously, as especially evidenced in the publications of Hansell, Turillazzi, and coworkers. However, much discussion of the evolutionary significance of the behavioral features treated in these works is confused, because of the lack of a phylogenetic perspective. The implications of the cladistic analysis of vespid subfamilies by Carpenter (1981) have not been properly appreciated, and no phylogenetic treatment of taxa below the subfamily level has been available. In the present work I address both of these issues. The conclusions of Carpenter (1981) are reiterated and extended, and a cladistic analysis of stenogastrine genera is presented. The results provide a point of departure for future evolutionary investigations of these wasps.

SUBFAMILY PLACEMENT

Carpenter (1981) provided the first cladistic analysis of any vespid taxon. The results of that study for subfamily relationships are shown in Figure 1. Stenogastrinae is the sister-group of Polistinae + Vespinae; Eumeninae is the sister-group of this component. This conclusion accords with traditional treatments such as Saussure (1852–1858) and Richards (1962), but is contrary to the views expressed by Richards (1971), Spradbery (1975) and van der Vecht (1977a). Richards (1971:486) observed that stenogastrines "are very different from other social wasps" in having a long pointed clypeus, long narrow mandibles and placement of the pronotal lobe halfway between the tegula and midcoxa. He stated that they "might even have evolved independently from some *Eumenes*-like, solitary ancestor." Spradbery presented a table comparing 17 "biological" characters for these four subfamilies. Finding that
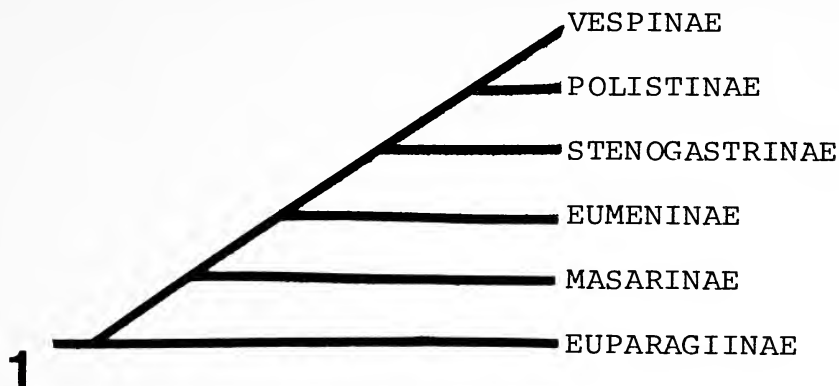
Fig. 1. Cladogram of vespid subfamilies after Carpenter (1981).

stenogastrines were in some respects intermediate between eumenines and the other social wasps, but also possessed of some unique features, he concluded that they "originated from an early vespoid ancestor," by which he meant that they were not closely related to other extant social wasps. This is shown by his statement "it would be unwise to look to the Stenogastrinae for examples illustrating intermediate steps in the achievement of social organization by higher Vespidae." These conclusions do not follow. Neither Richards nor Spradbery presented any evidence to indicate that hover wasps and other social wasps are not closely related phylogenetically. Their interpretations are based on Stenogastrinae being "different," that is possessing autapomorphies, as I have pointed out before (Carpenter, 1981). Autapomorphies (unique derived features) are irrelevant to phylogenetic placement — they merely demonstrate that the taxa possessing them are monophyletic (Hennig, 1966). Further, as will be shown, in the features listed by Spradbery in which the Stenogastrinae are intermediate between eumenines and higher social wasps, the similarity to the higher social wasps is derived while the similarity to the eumenines is primitive. Only derived similarity — synapomorphy — indicates close phylogenetic relationship (Hennig, 1966).

Van der Vecht (1977a) made a similar logical error. He listed eight characters in support of Richards' and Spradbery's interpretations, and although no attempt was made to polarize these characters into derived and primitive states, van der Vecht (1977a:58) concluded that:

"(a) The Stenogastrinae are so different from the Polistinae and the Vespinae, both in morphological and ethological characters, that a taxon consisting of these three groups cannot be regarded as monophyletic.

(b) The Stenogastrinae are likely to have evolved from a solitary cell-building ancestor with elongate gastral petiole.

(c) Several characters . . . suggest that this ancestor was more closely related to the Zethinae than to the Eumenini."

I (Carpenter, 1981) first treated the characters listed by van der Vecht in a phylogenetic context, polarizing them into primitive and derived states and showing that
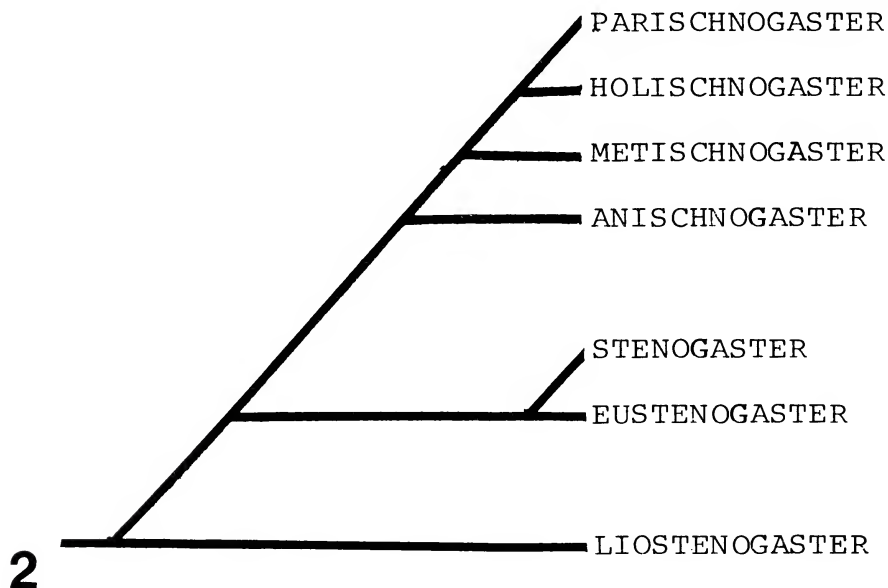
Fig. 2.   Cladogram of stenogastrine genera.

his conclusions did not hold. Three other characters established the sister-group relationship between Stenogastrinae and Polistinae + Vespinae (Fig. 1). However, several recent authors (e.g., Hansell, 1982b, 1983; Pardi and Turillazzi, 1982; Turillazzi, 1986a), although citing Carpenter (1981), nevertheless continue to cite van der Vecht to the effect that stenogastrines are closely related to eumenines. It is thus necessary to recapitulate the conclusions of my previous paper. Following this I shall adduce further evidence to support the subfamily cladogram in Figure 1.

The characters listed for the Stenogastrinae by van der Vecht (1977a), and the polarities established by Carpenter (1981) are:

(1) Acroglossal buttons lacking. These are present in all other vespid subfamilies except Euparagiinae. Apomorphic loss in Stenogastrinae is the parsimonious interpretation considering other characters (Carpenter, 1981:18). Since it is an autapomorphy, this character is irrelevant to the question of the interrelationships of Eumeninae, Stenogastrinae, Polistinae and Vespinae.

(2) Occipital carina running towards hypostomal carina. Van der Vecht considered this similar to the state of some *Zethus,* where there is a forked carina, with an evanescing branch running towards the mandible as well as the hypostoma. As I pointed out previously (Carpenter, 1981:18), this similarity is superficial. In the groundplan state of Vespidae as a whole there are two carinae (Carpenter, 1981). The dorsal one, running from the vertex towards the hypostoma (Figs. 3–6, 9), is the occipital carina of other Hymenoptera. A second carina extends from the mandibular base dorsad along the posterior eye margin in Euparagiinae and some Masarinae (Fig. 3). Richards (1962) termed this the "ventral occipital keel," but Snelling's (1986) term "postocular carina" is more descriptive. The complete carina reaching the
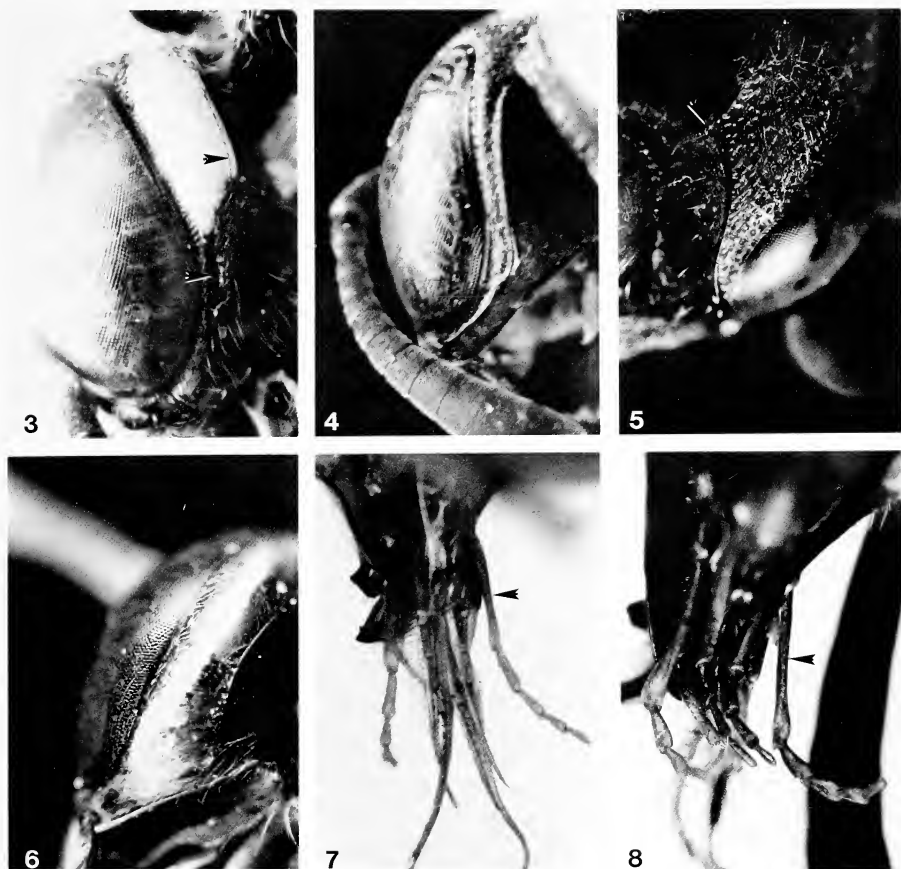
Figs. 3–8.   3–6. Lateral view of head. 3. *Metaparagia doddi* Meade-Waldo (Masarinae), 42×. The upper pointer indicates the occipital carina, the lower is on the postocular carina. 4. *Paramasaris brasiliensis* Giordani Soika (Masarinae), 50×. 5. *Zethus andinus* Brèthes (Eumeninae), 32×. Right side. The pointer indicates the branch running from the fused occipital and postocular carinae to the hypostomal carina. 6. *Liostenogaster nitidipennis,* 40×. 7–8. Palpi. The pointer indicates the second segment of the maxillary palpus. 7. *Anischnogaster iridipennis,* 50×. 8. *Eustenogaster* n. sp., 48×.

mandibular base seen in various solitary and social wasps is probably produced by confluence of these two carinae (Fig. 4), as suggested by Snelling for *Rolandia* (Masarinae), and this is the usual condition in Eumeninae. The forked carina (Fig. 5) found in most *Zethus* and closely related taxa does not occur in the genera usually considered relatively plesiomorphic in the "Zethinae," *viz. Discoelius, Protodiscoelius* and *Calligaster.* Therefore, the parsimonious interpretation is that a forked carina is probably apomorphic within Eumeninae, derived from a complete carina running to the mandibular base (Carpenter and Cumming, 1985:885 treated a forked carina as a groundplan state, but suggested that it could be considered as secondary). Under

either interpretation, the evanescing mandibular branch found in a few *Zethus* species is even further derived. Stenogastrinae possess none of these states, since they lack any trace of a postocular carina or forked composite carina (Figs. 6, 9). In fact, for their state to be synapomorphic with that found in species of *Zethus* with an evanescing mandibular branch, they would have to have originated as a subgroup of *Zethus* itself! No one has suggested this as a possibility, yet this is required for van der Vecht's interpretation to hold.

(3) Mandibles elongate and sometimes decussate, tridentate in females and "often more or less reduced" in males (Figs. 22–23). Pardi and Turillazzi (1982:19), following van der Vecht, stated that the mandibles of stenogastrines showed "concordance" with those of eumenines. Carpenter (1981:17) pointed out that decussate mandibles are plesiomorphic in Vespidae, and that all the subfamilies overlap in mandibular length. The tridentate condition is an autapomorphy. Both van der Vecht (1977a) and Carpenter (1981) noted that the mandibles are usually 4- or 5-toothed in Eumeninae (including "Zethinae"), Polistinae and Vespinae; this is also the case in Gayellini. The "reduced" male mandibles are not a groundplan character of the subfamily, but instead are apomorphic in particular genera (see below). This character therefore does not support van der Vecht's conclusions; it is uninformative on relationships.

(4) Clypeus pointed apically in female, but lateral angles not projecting as in Polistinae (cf. Figs. 11 and 12). This is simply another autapomorphy (state 21c in Carpenter, 1981), and so uninformative. It is not similar to that of Eumeninae, contrary to Pardi and Turillazzi (1982). The clypeus is primitively truncate in the Eumeninae (Fig. 12; cf. Carpenter and Cumming, 1985), and is truncate or emarginate in nearly all species, being pointed only in a few derived taxa (e.g., *Rhynchalastor*).

(5) Antennal sockets far apart and separated from clypeus by long supraclypeal area (Figs. 21–22). I (Carpenter, 1981:19) did not deal with this state specifically, but stated "In the plesiomorph condition the anterior tentorial pits are close to the antennal sockets and the dorsal margin of the clypeus runs more or less straight between them." The state of a long supraclypeal area is unique to Stenogastrinae as a groundplan feature, and therefore is another autapomorphy, and so uninformative.

(6) Forewing marginal cell with RS almost straight (Fig. 13), hindwing with only two closed cells (Fig. 15). Only the second character was mentioned specifically by me (Carpenter, 1981), and I showed it is an autapomorphy of Stenogastrinae (only females were mentioned, but it is also true of males). The forewing character is also unique to Stenogastrinae, and so also an autapomorphy. Both characters are thus uninformative.

(7) Male genitalia, particularly the aedeagus and volsella, "are rather different from those of other diplopterous wasps, but are perhaps most similar to those of Zethinae." I (Carpenter, 1981:22) discussed both the aedeagus and volsella more extensively, pointing out that both differed in detail in the two groups and that "Zethinae" were in fact more similar to Eumeninae. The condition in Stenogastrinae is autapomorphic.

(8) Pupal metasoma strongly bent at the articulation of segments I and II. Van der Vecht stated that this was also true of some *Zethus* species—but also some *Eumenes* s.l. Thus, it cannot show closer relationship of Stenogastrinae to "Zethinae" than to Eumenini (i.e., *Eumenes* s.l.), contrary to both van der Vecht (1977a) and Pardi and
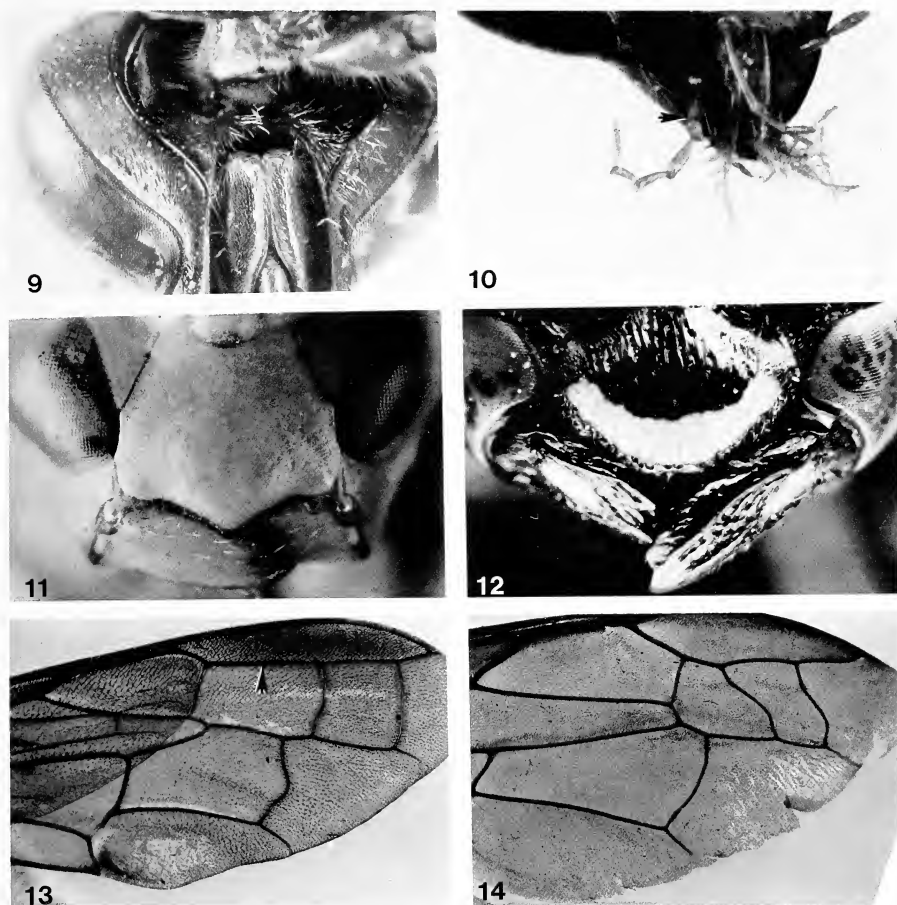
Figs. 9–14. 9. *Eustenogaster luzonensis,* 28×. Ventral view of head. 10. *Parischnogaster depressigaster,* 44×. Palpi. The pointer indicates the second segment of the maxillary palpus. 11–12. Clypeus. 11. *Polistes xantholeucus* van der Vecht, 40×. 12. *Discoelius zonalis* (Panzer), 40×. 13–14. Forewing. 13. *E. eximia,* 15×. The pointer is in the second submarginal cell, and points to the RS vein. 14. *Dolichovespula maculata* (L.), 12.6×.

Turillazzi (1982). I (Carpenter, 1981:23) considered it convergent in species with long petioles.

None of these characters supports van der Vecht's conclusions; they are all un-informative on relationships. Most are autapomorphies, which, to be sure, do show that the Stenogastrinae is "so different" from Polistinae and Vespinae. But mere degree of difference indicates nothing about phylogenetic relationship (Hennig, 1966). These characters indicate only that the Stenogastrinae are truly monophyletic, which no one has questioned anyway. Carpenter (1981) cited three synapomorphies for

Stenogastrinae + (Polistinae + Vespinae): forewing marginal cell pointed onto costa (cf. Figs. 13 and 14), larval labrum not narrowed where it joins the clypeus and narrower than maximum width of clypeus, and the behavior of simultaneous progressive provisioning. All of these characters show some homoplasy (see Carpenter, 1981), but none of the characters cited by Richards, Spradbery or van der Vecht contradict this relationship—their characters simply say nothing about it. A related point is worth making. For van der Vecht's suggestion of closer relationship of Stenogastrinae to "Zethinae" than to Eumenini to be valid, not only would the three social wasp synapomorphies have to be convergent—but so would the autapomorphies of the Eumeninae as a whole. Carpenter (1981:26) cited four characters whose polarity could be clearly established which showed the monophyly of the Eumeninae as a whole. These are the parategula, hindcoxal carina, bifid claws and the shape of the larval labrum. For Stenogastrinae to be closely related to "Zethinae" they would have to be a subgroup of Eumeninae, and all of these features would either have to have been secondarily lost in Stenogastrinae or convergently gained at least twice in Eumeninae. There is no evidence whatsoever which compels the inference of such a massive degree of homoplasy, that is, no characters which actually suggest close relationship between hover wasps and a subgroup of potter wasps.

Before leaving this subject, I will point out additional behavioral characters which support the placement of the Stenogastrinae shown in Figure 1. As mentioned previously, all three social wasp subfamilies exhibit simultaneous progressive provisioning, that is a female tends several growing larvae. In all three groups, the female tends the larvae into the pupal stage, with females of Stenogastrinae removing the meconium after the pupal moult (Spradbery, 1975; Turillazzi, 1985b). Females of potter wasps which convergently show simultaneous progressive provisioning (species of *Synagris,* cf. Roubaud, 1911) do not show such extended care; they do not tend into the pupal stage. Second, Spradbery (1975) characterized the provisioning behavior in hover wasps as "intermediate" between the mass provisioning of potter wasps and the progressive provisioning of other social wasps. By this he meant that the amount of food provided in Stenogastrinae was sufficient to last a day or more. Mass provisioning is clearly primitive in Vespidae and progressive provisioning derived (Carpenter, 1981), thus stenogastrines may be considered more similar to higher social wasps, in showing a form of progressive provisioning, than potter wasps (mass provisioning). The form of this behavior in hover wasps may be the primitive condition. This character was interpreted by Pardi and Turillazzi (1982) as showing phylogenetic relationship between Stenogastrinae and Eumeninae, but as is obvious from the foregoing, this is a misinterpretation based on symplesiomorphy. Symplesiomorphy—the sharing of primitive features—is completely uninformative phylogenetically (Hennig, 1966). Third, all three social wasp subfamilies build complete nests, hanging free from the substrate except for the attachment point in the ground-plan condition (convergent in a few species of Eumeninae, Carpenter and Cumming, 1985; the astelocyttarus condition found in some paper wasps is a further modification, since the primitive genera do not show this trait). The primitive condition in Vespidae is burrowing in the ground or using pre-existing cavities as a burrow. Another character in Spradbery's list can be interpreted as a fourth behavioral synapomorphy of the three social wasp subfamilies. This is whether two or more females

are present on a newly founded nest, characterized by Spradbery as not occurring in Eumeninae (it actually does occur in a few species; cf. West-Eberhard, 1978), "frequent" in Stenogastrinae, "common" in Polistinae and "'rare" in Vespinae. In the evolutionary model for the origin of social behavior of West-Eberhard (1978), the condition of nest-sharing corresponds to the primitively social stage. Polistinae + Vespinae, being all eusocial, are inferred to have a common ancestor which evolved through a stage of casteless nest-sharing. Therefore, if the ground-plan condition in Stenogastrinae is nest-sharing, this would be another synapomorphy of these three groups. Stenogastrinae are still frequently characterized as having solitary species (e.g., Hansell, 1982a; Pardi and Turillazzi, 1982; Ohgushi et al., 1983a), although as noted above they are actually at least subsocial (Iwata, 1967, 1976). But many species do not consistently exhibit nest-sharing. For example, in *Stenogaster concinna* (Spradbery, 1975), *Eustenogaster calyptodoma* (Hansell, 1987), *Parischnogaster mellyi* (Hansell, 1982a, 1983), *Holischnogaster gracilipes* (Hansell, 1986a), and *Liostenogaster flavolineata* (Hansell et al., 1982) colonies with only a single female are common. But in all of these species, multiple-adult nests also occur. Thus, on present evidence, nest-sharing appears to be universal in the subfamily, but it does not characterize the entire colony cycle (as is also the case in many Polistinae and Vespinae). The single female nests found in these species may have been recently founded, since a single foundress appears to be the general mode of colony foundation (cf. references above, and Krombein, 1976; Yamane et al., 1983a, b; Turillazzi, 1982, 1985a). Other adults are then added either by emergence of daughters which remain on the natal nest for a period (e.g., Spradbery, 1975; Krombein, 1976; Hansell, 1983, 1986a, 1987; Turillazzi, 1985a) and/or joining behavior (e.g., Yoshikawa et al., 1969 but cf. Hansell, 1982b; Hansell et al., 1982; Turillazzi, 1985a, c). At the very least, facultative nest-sharing is then most parsimoniously inferred to be the ground-plan state of Stenogastrinae as a whole. As such it is a synapomorphy of all the social wasps, for assuming West-Eberhard's model (cf. Carpenter, 1988) it is then most parsimoniously inferred to be the ground-plan state of their common ancestor. Other behavioral similarities are probably synapomorphies of Stenogastrinae + Polistinae + Vespinae as well (see below).

These interpretations of behavioral data are contrary to those of authors such as Pardi and Turillazzi (1982) and Turillazzi (1985a, b, 1986a), who argue that the similarities in social behavior among Stenogastrinae and Polistinae + Vespinae are convergent. But this view only followed from van der Vecht's scheme of phylogenetic relationships, which these authors adopted. As discussed above and in Carpenter (1981), that scheme is untenable. The available evidence best supports the cladogram of Figure 1, and so the development of social behavior in stenogastrines is not independent of that in the other social wasp subfamilies. Evolution subsequent to the diversification of their common ancestor has produced differences in various details of the social behavior of these three groups, but where behavioral similarities occur in the groundplans of the subfamilies, such similarities must be inferred to be the product of common ancestry (Hennig, 1966; Farris, 1983). As Carpenter (1981: 30) stated: "Exclusion of the stenogastrines from discussion of social behaviour in the Vespinae + Polistinae may lead to the loss of valuable evolutionary perspective." The reverse is equally true.

GENERIC RELATIONSHIPS

Materials and Methods

The characters studied were drawn from those used by previous authors of taxonomic or behavioral papers on these wasps. Autapomorphies of the subfamily already discussed by Carpenter (1981) were not included. The 24 adult morphological characters discussed below were examined on pinned specimens; all are deposited in the Museum of Comparative Zoology, U.S. National Museum, or Australian National Insect Collection. The species examined are listed in the appendix. Male genitalia were dissected, slightly cleared in lactophenol, and examined in glycerin. Illustrations were made with a Wild M-400 photomacroscope and Kodak T-Max 400 film. Morphological terminology is as in Carpenter (1981) and Carpenter and Cumming (1985). Larvae of *Liostenogaster flavolineata, Eustenogaster calyptodoma, Holischnogaster gracilipes* and *Parischnogaster striatula* were provided by Dr. M. H. Hansell. Larvae of *E. eximia, E. hauxwellii, E. micans, P. mellyi* and *P.* spp. in the collection of the British Museum were also studied. Data on other species were drawn from the literature as noted. Behavioral data were also drawn from the literature.

Character polarities were established by considering all other vespid subfamilies as outgroups. The ten morphological characters which varied among the genera (that is, were informative concerning relationships) were coded as in Tables 1 and 2, and subjected to quantitative cladistic analysis. This was performed using the PHYSYS® system by J. S. Farris and M. F. Mickevich, State University of New York at Stony Brook and Maryland Center for Systematic Entomology, as implemented on the VAX 11/780 computer running VMS at Harvard University. The behavioral characters were analyzed separately because of the ambiguity of many of these features. As shown below, at the generic level they are congruent with the morphological results.

CHARACTERS

The Wings

1. Forewing second submarginal cell (IRS). In other Vespidae (Fig. 14) the anterior border of the second submarginal cell (formed by the RS vein) is much shorter than the posterior border (formed by the M vein). Only in Stenogastrinae are the anterior and posterior borders of approximately equal length, giving a rectangular appearance to the cell (Fig. 13). This unique feature is found in all Stenogastrinae, and so is an autapomorphy of the subfamily.

2. Hindwing. In males of the genus *Eustenogaster* (Fig. 15) there is a pigmented area along the posterobasal edge of the hindwing proximal to the preaxillary excision (edge of the clavus of Wootton, 1979). This character was mentioned in the diagnosis of this genus by van der Vecht (Yoshikawa et al., 1969:165). It is unique to *Eustenogaster,* and so is an autapomorphy, showing the monophyly of the genus. *Eustenogaster* males also lack the short fringe of hairs found along the posterior edge of the wing in other vespids. This fringe of hairs becomes greatly elongated in *Metischnogaster* (Fig. 16), and is an autapomorphy of that genus. In female *Metischnogaster* the hairs are moderately longer than in other hover wasps, but in males they are longer than the distance between vein 1A and the posterior margin of the wing.
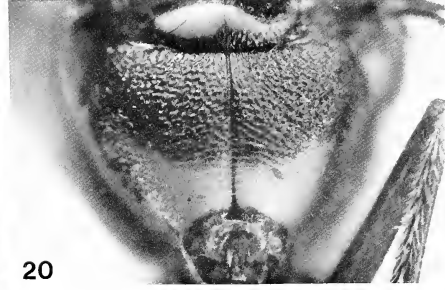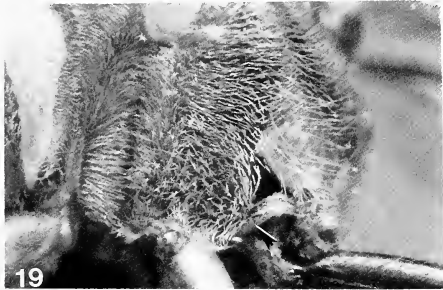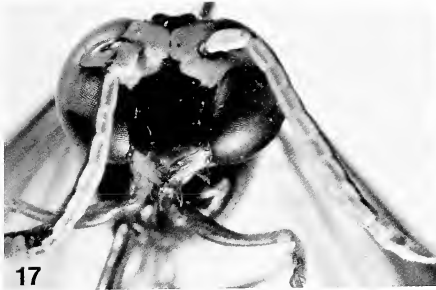
Figs. 15–20. 15. *Eustenogaster fulvipennis,* 22×. Hindwing. The pointer indicates the posterobasal pigmented area. 16. *Metischnogaster cilipennis* (Smith), 32×. Lateral view of metasoma. The pointer indicates the elongate fringe of hairs on the hindwing. 17. *M. cilipennis* male, 20×. 18–19. The pointer indicates the propodeal valvula. 18. Liostenogaster nitidipennis, 19×. Lateral view of metasoma. 19. *Parischnogaster depressigaster,* 40×. Lateral view of propodeum. 20. *Anischnogaster spilaspis,* 34×. Posterior view of propodeum.

Head

3. Occipital carina. In *Liostenogaster* the occipital carina runs towards the hypostomal carina but evanesces before reaching it (Fig. 6). There is no trace of the postocular carina, which is derived. In all other stenogastrine genera the occipital carina reaches the hypostomal carina and fuses with it (Fig. 9). This is a further derived condition, and so this state is a synapomorphy grouping all the genera apart from *Liostenogaster*.

4. Male clypeus. As mentioned above, in female Stenogastrinae the clypeus is

pointed apically. This is also true of males in most of the genera (Figs. 17, 21), although the pointing is not generally as pronounced as in females. In *Stenogaster* the male clypeus is rounded apically, so that it appears broadly rounded (Fig. 22). The clypeus is also depressed apically. This state is clearly apomorphic, but is approached in *Eustenogaster.* In that genus (Figs. 23 is the least developed condition) the males have the clypeus apically rounded into a blunt angle, but the condition is not as different from the female, and the clypeus is not depressed apically. Males of a few other species have the clypeus slightly rounded apically (*Parischnogaster depressigaster, Anischnogaster dubia*), but other species in these particular genera have a pointed clypeus. An apically rounded clypeus in the male may therefore be treated as a synapomorphy between *Stenogaster* and *Eustenogaster,* with the ventral depression being an autapomorphy of *Stenogaster.*

5. Male mandibular teeth. As noted above, tridentate mandibles are an autapomorphy of the subfamily. Reduction from this number in males of some of the genera is then further apomorphic. This occurs in *Metischnogaster,* where the mandibles are bidentate. It also occurs in an undescribed species of *Liostenogaster.* In *Anischnogaster* the proximal teeth are quite blunt, appearing almost fused in some species (*A. iridipennis* and *loriai*; cf. figs. in van der Vecht, 1972). But the most notable reduction occurs in *Stenogaster* and *Eustenogaster,* where both of the proximal teeth are lost (Figs. 22, 23). Traces of a proximal tooth remain in *Eustenogaster,* in the form of a blunt inner angle (Schulthess, 1914: fig. B), but in *Stenogaster* even this is lost and the mandible is narrowed and curved apically (Fig. 22). Reduction to one tooth is thus a synapomorphy of *Eustenogaster* + *Stenogaster,* with distal narrowing and curving an autapomorphy of the latter genus. The bidentate mandibles of *Metischnogaster* are an autapomorphy of that genus, but the relationship between this state and the unidentate condition is unclear. Although it seems straightforward to treat the states as part of a linear transformation series, as in Table 1, the results of analysis with other characters (Fig. 2) require homoplasy under this interpretation. The transformation in *Metischnogaster* occurs independently of that in the common ancestor of *Eustenogaster* + *Stenogaster.* It would be more parsimonious to treat both the bidentate and unidentate conditions as arising independently from the tridentate state. The initial coding of this character (Table 1), however, does not affect the results other than to introduce some homoplasy, so it is retained here.

6. Labial palpi. In the Stenogastrinae, the first segment of the labial palpus is greater than or approximately equal to the combined length of segments 2–4 (Fig. 8; figs. in van der Vecht, 1975, 1977a). The general condition in Vespidae as a whole is to have the two basal segments of approximately equal length. Therefore, the condition in hover wasps is derived, and so is another autapomorphy of the subfamily. As stated by Schulthess (1914:254), the first segment is relatively longer in *Eustenogaster* + *Stenogaster* than in the rest of the subfamily.

7. Maxillary palpi. In Vespidae as a whole the segments of the maxillary palpus are all of approximately equal length. This is the groundplan condition, but in hover wasps segment 2 is frequently elongate. In *Liostenogaster, Holischnogaster* and *Anischnogaster* it ranges in length from 1.5 to about twice the length of segment 3 (Fig. 7; van der Vecht's 1977a key is misleading in regard to latter genus, but his 1972 revision characterizes the feature correctly). In *Stenogaster* and *Eustenogaster* (Fig. 8) it is three times or more the length of segment 3 and about equal to or greater

Figs. 21–26. 21–23. Clypeus of male. 21. *Holischnogaster gracilipes,* 48×. 22. *Stenogaster concinna,* 32×. 23. *Eustenogaster hauxwellii,* 34×. 24–26. Antennae. 24. *Parischnogaster depressigaster* female, 25×. 25. *H. gracilipes* male, 20×. 26. *S. concinna* male, 16×.

than the combined length of segments 3–6. However, in *Parischnogaster* and *Metischnogaster* (Fig. 10) segments 2 and 3 are of approximately equal length. Therefore, if elongation of segment 2 is an apomorphic groundplan feature of Stenogastrinae, it has undergone some reversal. It may be better to regard the elongation as an apomorphic tendency arising several times, since the differences between most of the genera are not very great. However, this is not true of the greater elongation of segment 2 in *Eustenogaster* + *Stenogaster*; this is clearly a distinguishing feature, as realized by Schulthess (1914:254). It is another synapomorphy of these two genera.

8. Antennae. Several modifications of the antennae are found in hover wasps. The antennae are usually somewhat swollen apically, but flagellomere 8 (females) or 9 (males) is usually less than twice the width of flagellomere 2. However, in *Holischnogaster* and *Parischnogaster* (Figs. 24, 25) the swelling is more extreme, so that flag-

Table 1.   Informative characters and their inferred polarities as coded in alphanumeric format for the CREAD input command of PHYSYS. The plesiomorphic state is leftmost. States separated by commas are considered to have evolved separately from the plesiomorphic state.

3. Occipital carina:	GAP-FUSED
4. Male clypeus:	POINT-ROUND
5. Male mandibular teeth:	THREE-TWO-ONE
7. Maxillary palpi:	EQUAL-GREATER
8. Antennae:	NORMAL-CLUB,FLAT,TIPPED
14. Propodeal valvula:	ROUND-NARROW
16. Propodeal sculpture:	STRIATE-SMOOTH,PUNCTATE
20. Segment II:	NORMAL-PETIOLE
22. Parameral spine:	SPINOSE-FLAT
24. Aedeagus:	NORMAL-DILATED

ellomere 8 or 9 is much more than twice the width of the second flagellomere. This is a synapomorphy of these two genera, but the state is approached in a few other species (e.g., *Anischnogaster spilaspis*), somewhat weakening it. Other modifications are autapomorphies of two other genera. In *Metischnogaster* (Fig. 17) the flagellomeres are noticeably flattened ventrally in the male, and in *Stenogaster* (Fig. 26) the apical flagellomere of the male is truncate and flattened, as well as often dilated (figures in van der Vecht, 1975).

9. Vertex. As noted by van der Vecht (1977a) in his description of the genus, *Metischnogaster* has an impressed median longitudinal groove on the vertex between the ocelli and occipital carina. Although a faint impression sometimes appears in other hover wasps, none have a clear line, and so this feature is an autapomorphy of *Metischnogaster*.

Mesosoma

10. Pronotum. Hover wasps lack the dorsal pronotal carina and pretegular carina which are found in the groundplans of all other vespid subfamilies. These losses are autapomorphic, further confirming the monophyly of the Stenogastrinae.

11. Notauli. In *Metischnogaster* there are distinct, deeply impressed notauli on the scutum (van der Vecht, 1977a, termed them prescutal furrows). Although this seems similar to the primitive hymenopterous condition, other stenogastrines lack notauli — shallow traces occur only in some species of *Parischnogaster* (*P. depressigaster* and *nigricans*) and *Anischnogaster*. Therefore, the deeply impressed condition in *Metischnogaster* is probably apomorphic, not primitive. As such this character is an autapomorphy of the genus.

12. Male metapleuron. Van der Vecht (1977a) called attention to the fact that in males of *Metischnogaster* the metapleuron and part of the mesepisterum and propodeum are sunken and densely pubescent, and this area is bordered posteriorly by a strong carina (Fig. 16). This is an outstanding autapomorphy of the genus. Some species of *Parischnogaster* have dense pubescence on this part of the mesosoma (Fig. 19), but this is not similar.

13. Scutellum. Van der Vecht in the diagnosis of *Eustenogaster* (Yoshikawa et al.,

1969) used the character of the scutellum with a sharp, median longitudinal carina as a distinguishing feature. This is an autapomorphy of the genus. Other stenogastrines have at most faint traces of such a carina anteriorly.

14. Propodeal valvula. The relatively large propodeal valvula of *Eustenogaster* was noted by Carpenter (1981:20). A similar, albeit smaller, valvula is found in *Liostenogaster, Stenogaster* and *Anischnogaster* (Fig. 18). It is also narrower in the latter two genera. No submarginal carina is present in stenogastrines, but the valvula is well differentiated from the propodeum, appearing similar to the groundplan condition in Eumeninae and other social wasps. In *Metischnogaster, Holischnogaster* and *Parischnogaster* the valvula is much narrower (Fig. 19). In *Metischnogaster* it is essentially completely reduced; in *Holischnogaster* and *Parischnogaster* it is completely attenuate only posteriorly, and narrow but present anteriorly. The state of a posteriorly reduced valvula is thus a synapomorphy of these three genera, with further reduction autapomorphic in *Metischnogaster*.

15. Propodeal orifice. One of the distinguishing features of *Stenogaster* is a raised lamella on the propodeum just dorsal to the propodeal orifice (Fig. 27). This is not similar to the condition in other Vespidae where there may be a submarginal carina or a continuation of the propodeal valvula above the orifice; the lamella in *Stenogaster* is completely separated from the propodeal valvula. The state in *Stenogaster* is unique, and so an autapomorphy of the genus.

16. Propodeal sculpture. There are various forms of sculpturing on the propodeum in Vespidae. Most species have the propodeum punctate, and the punctation may be quite coarse. Transverse ridges on the posterior face of the propodeum are also quite common, as in *Polistes*. There are three states in the Stenogastrinae. In *Stenogaster, Metischnogaster, Holischnogaster* and some species of *Parischnogaster* (e.g., *P. depressigaster* and *timida*) there are transverse ridges on the posterior face of the propodeum (Figs. 27, 28). The ridges may be quite weak, as in *Stenogaster* (Fig. 27). In *Anischnogaster* and other species of *Parischnogaster* (Fig. 20) there are no ridges, but the punctation is well developed, and irregular transverse rugae may somewhat resemble the ridges found in other stenogastrines. In *Liostenogaster* and *Eustenogaster* (Fig. 18) the propodeum is smooth and shining, lacking both ridges and punctation (although pubescent). This last state is clearly derived, as it is relatively uncommon in Vespidae and does not characterize the groundplan of any of the other subfamilies. But the transformation series of the character as a whole is unclear. Either a striate or punctate propodeum is plesiomorphic in the subfamily, but it is not obvious which, especially considering that *Parischnogaster* is variable in this regard. The outgroups are variable as well, although the punctate condition is the more general. Any interpretation requires homoplasy, but considering that the striate condition occurs in "groups otherwise having little in common" (Kluge and Farris, 1969; cf. Farris, 1982), that is, several genera separated on the cladogram (Fig. 2), it is treated here as the plesiomorphic condition. The punctate condition in *Anischnogaster* is then an autapomorphy, convergent in some *Parischnogaster* (note that under any interpretation, given the cladogram of Figure 2, the striate condition must be treated as the groundplan state of the latter genus). A smooth propodeum is also convergent; as shown by Figure 2 other characters indicate that *Liostenogaster* and *Eustenogaster* are not closely related.

17. Male foreleg. Pagden (1958: fig. 21b) showed the row of peculiar spatulate setae

on the underside of the foretibia in males of *Metischnogaster,* first noted by Smith (1857). Pagden also figured (1958: figs. 21c, d) the ventral production of some of the fore tarsomeres into spines in males of this genus. Both states are autapomorphies of *Metischnogaster,* being unique.

18. Male midleg. Van der Vecht (1977a) used the condition of asymmetrical mid-tarsi of males in *Parischnogaster* as a key character in distinguishing the genus. It is autapomorphic, unique in the subfamily. Absence of this condition was a major reason for van der Vecht's distinction (1977a:73) of *Holischnogaster* as a separate genus, for, as he stated, it is closely related to *Parischnogaster.*

Metasoma

19. TII spiracles. In *Metischnogaster* (Fig. 31) the spiracles of metsomal segment II are visible in dorsal view, whereas they are only visible laterally in other hover wasps. This is an autapomorphy of *Metischnogaster*; it is unique.

20. Segment II petiole. In *Anischnogaster, Metischnogaster, Holischnogaster* and *Parischnogaster,* metasomal segment II is distinctly petiolate basally (Figs. 31, 32). A similar state occurs in various Eumeninae (e.g., *Paramischocyttarus*) and Polistinae (*Belonogaster*), but is not ancestral for either subfamily. Thus a petiolate segment II is derived in Stenogastrinae. In *Liostenogaster, Eustenogaster,* and *Stenogaster* segment II is not petiolate, but merely narrowed basally (Fig. 30). This is the primitive condition for the subfamily, and so a petiolate segment II is a synapomorphy for *Anischnogaster* + (*Metischnogaster* + (*Holischnogaster* + *Parischnogaster*)).

21. Male SVII. In male Stenogastrinae, the sternum of metasomal segment VII is noticeably flattened, whereas the usual condition in Vispidae is to have it rounded as in females. The state in Stenogastrinae is thus another autapomorphy of the subfamily.

Male Genitalia

Certain stenogastrine autapomorphies in the male genitalia were discussed by Carpenter (1981:22, 27). These were the volsella with the digitus curved apically and desclerotized proximally, and the aedeagus very attenuate apically with the ventral processes small and narrow.

22. Parameral spine. In *Holischnogaster* and *Parischnogaster* the parameral spine is greatly dilated basally (Figs. 29, 33), so that its height is nearly equal to that of the paramere in lateral view. This character was noted by Schulthess (1914: figs. G and H), and was used as a key characteristic by van der Vecht (1977a). Charnley (1973:55–56) misinterpreted the dilated spine as a subdivision of the paramere. The state is unique in the Vespidae, which typically have the spine elongate (Fig. 34), and so is an outstanding synapomorphy of *Holischnogaster* + *Parischnogaster.*

23. Volsella. The cuspis and lamina volsellaris appear completely fused in Steno-gastrinae (Figs. 35, 36). This is a derived condition in Vespidae, which has arisen in several subfamiles (Carpenter, 1981). The cuspis is more or less rounded apically and the digitus scimitarlike and completely reduced proximally (Fig. 35; it remains a separate structure, contrary to what is depicted in van der Vecht, 1977a: fig. 26). The form of the volsella differs mostly in minor detail among the genera, except in
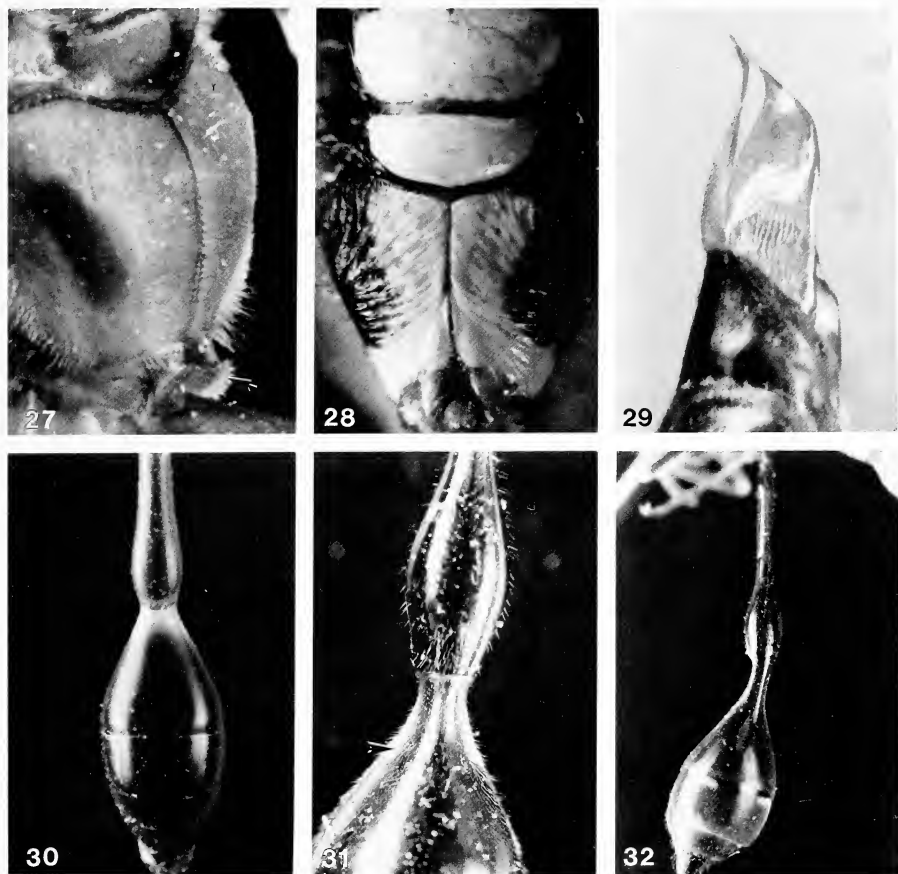
Figs. 27–32. 27–28. Propodeum. 27. *Stenogaster concinna,* 46×. Lateral view. The pointer indicates the lamella dorsal to the propodeal orifice. 28. *Metischnogaster drewseni,* 60×. Posterior view. 29. *Parischnogaster nigricans* male, 50×. Parameral spines. 30–32. Metasoma. 30. *S. concinna,* 14×. 31. *M. drewseni,* 32×. The pointer indicates the spiracle on Tergum II. 32. *P. mellyi,* 14×.

Stenogaster. In this genus, the cuspis + lamina is strongly narrowed medially (Fig. 36). This is a unique derived condition, another autapomorphy of *Stenogaster.*

24. Aedeagus. In *Metischnogaster* the aedeagus has a pair of small projections located laterally and subapically. In *M. cilipennis* they are blunt (van der Vecht, 1977a: fig. 27) but in *M. drewseni* they are sharp and toothlike (van der Vecht, 1977a: fig. 37). Such projections are not found elsewehre in the Stenogastrinae, and so their presence is another autapomorphy of *Metischnogaster.* Another feature of the aedeagus may be a synapomorphy of *Metischnogaster* + (*Holischnogaster* + *Parischnogaster*). In these genera, the aedeagus is apically strongly compressed, and the apex is dilated in lateral view (Fig. 37; van der Vecht, 1977a: figs. 27, 37, 47). The dilation
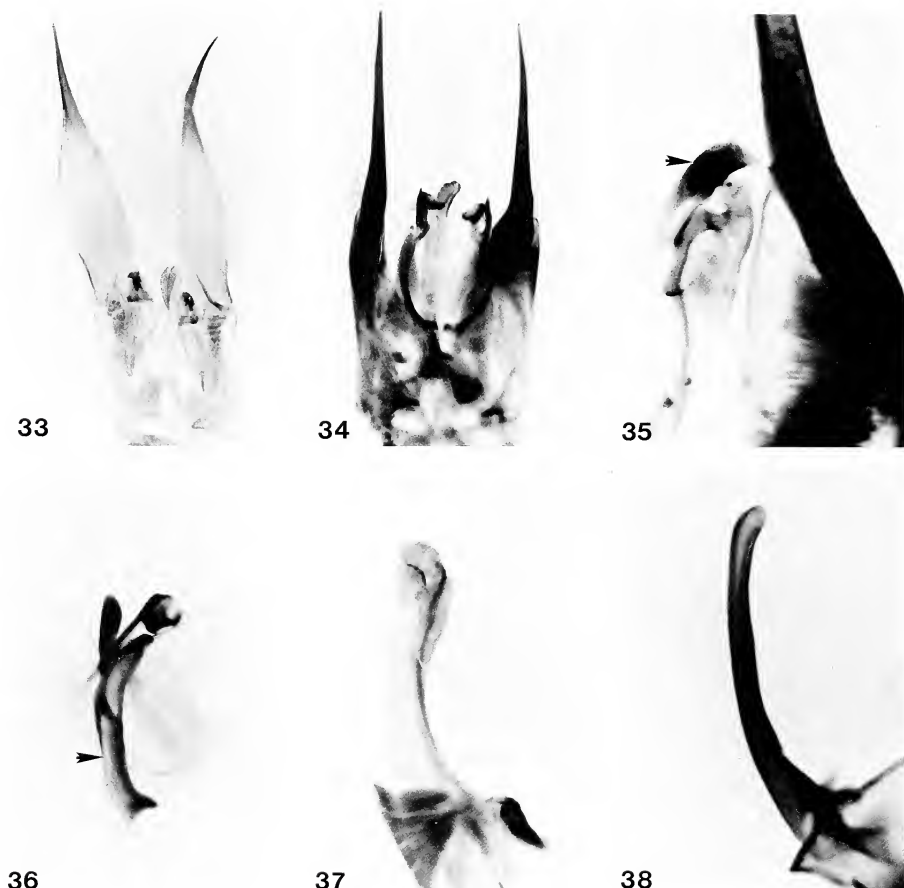
Figs. 33–38. Male genitalia. 33–34. Ventral view. *Holischnogaster gracilipes,* 40×. 34. *Stenogaster adusta,* 38×. 35–36. Lateral view of volsella. 35. *Eustenogaster eximia,* 64×. Right side. The pointer indicates the digitus. 36. *S. adusta,* 64×. Left side. The pointer indicates the lamina volsellaris. 37–38. Lateral view of aedeagus. 37. *Metischnogaster cilipennis,* 64×. 38. *S. concinna,* 64×.

is least pronounced in *Parischnogaster mellyi* among the species I have examined, where the apex is just slightly thickened. The generality of this character should be checked further in other species of *Parischnogaster,* but the condition does not occur in other hover wasps (Fig. 38), and so is treated here as a synapomorphy of the three genera showing it.

Larvae

Use of the larvae as a source of taxonomic characters continues to be hampered by the paucity of descriptions. Thanks to M. H. Hansell, I have been able to examine specimens of one genus for which the larvae are undescribed (*Holischnogaster*), but

no material or description of species of *Metischnogaster* or *Anischnogaster* have been available. I have therefore not attempted to make a very exhaustive study of the larvae, but only provide here some general descriptive notes.

The general form of the larva is basically as in other Vespidae: fusiform, unpigmented except for the head capsule and mandibles, ecdysial line and parietal bands present, galeae and palpi conical and somewhat projecting, spinneret a transverse slit without raised lips, 10 circular spiracles present, spiracular atria unarmed, pleural lobes present, anus a straight terminal slit. The first spiracle is about twice the diameter of the succeeding spiracles, as occurs in some Polistinae. Abdominal segments 1–6 have prominent dorsal lobes. The presence of long setae on the prothorax is an autapomorphy of the subfamily (Carpenter, 1981). Characters of the head and mouthparts are further discussed below.

It should be noted here that several recent authors have stated that a distinguishing feature of Stenogastrinae is a reduced number of larval instars. The condition in other Vespidae which have been studied is five, e.g., Vespinae (Spradbery, 1973) and the eumenine *Ancistrocerus antilope* (Cooper, 1966). Five instars have also been reported in Stenogastrinae (Iwata, 1967). However, Hansell (1982a, 1986a) and Turillazzi (1985b) have suggested that there are only three or four instars, which if true would be an autapomorphy, but neither author established this. They simply cited frequency distributions of head capsule widths, with Hansell (1982a) citing "Dyar's rule" on the geometrical size progression of head widths of instars—although he also cited Richards (1949) to the effect that the rule does not hold in general. Both Hansell and Turillazzi disputed Iwata's partitioning of his own data into five instars only by arguing that the measurements fit as well or better into fewer size classes. But as pointed out by Cooper (1966), for definitive demonstration of the number of larval instars three conditions must be satisfied:

"(1) the first instar larva must be identified with certainty, generally by witnessing hatching, (2) exuvia must be removed when shed, or very shortly thereafter, and (3) closely and appropriately spaced observations must be continued from hatching to the emergence of the imago."

None of these conditions were met in Hansell's or Turillazzi's cited papers. It is possible that the earliest instars were lumped together; as shown by Buysson (1903) and Cooper (1966) the first instar may not even shed the chorion until the first moult in Vespidae. Although the hatching sequence and immediate shedding of the chorion has been observed in *P. mellyi* by Turillazzi (1985d), study of other species is required to establish the generality of this in Stenogastrinae. And collection of exuvia is required to ascertain the number of larval instars with complete certainty. At present there is no clear case for accepting that a reduced number occurs.

25. Head. A labrum narrower than the maximum width of the clypeus and not narrowed where it joins the clypeus is a synapomorphy uniting the three social wasp subfamilies (Carpenter, 1981), although some polistines show reversal of this feature. All the stenogastrine species with undescribed larvae which I have examined also show this character, the labrum being just over half the width of the clypeus. The ventral margin of the labrum is truncate to slightly bisinuate but not bilobed as it is in Vespinae. The clypeus is much wider than high, as is usually the case in Vespidae, and the frontoclypeal suture is well developed. The anterior margin of the clypeus

is well below the level of the mandibular bases. *Liostenogaster flavolineata* differs from the other stenogastrine species examined in having the entire head capsule pigmented, whereas the pigmentation is confined to the lower part of the head capsule in the other species. It is unclear whether any significance should be attached to this.

The most notable feature by which larval Stenogastrinae differ from other Vespidae is in the presence of an antennal papilla. This is an elongate projection in all species examined; other vespids have sensilla on the antennal plate. Other Aculeata show considerable variation in the presence of papillae or sensilla on the antennal plate (Evans, 1987), and so a papilla may not be homologous as a primitive feature among aculeate families. But even if it is, the presence of one in Stenogastrinae is then an apomorphic reversal, since the subfamily is relatively derived in the Vespidae (Fig. 1; Carpenter, 1981).

26. Mouthparts. Iwata (1967) stated that the mandible of the stenogastrines he examined was bidentate, and his figs. 6 and 9 for *Liostenogaster nitidipennis* and *Parischnogaster mellyi* appear to show this, but it is incorrect. As Richards (1978: 14) stated, the larval mandibles are tridentate in stenogastrines, with one of the teeth smaller and set back on the dorsal margin (as figured for *Stenogaster concinna* by Spradbery, 1975; fig. 10). Tridentate mandibles are general in the species I have examined, including *P. mellyi*; this is plesiomorphic in the Vespidae (Carpenter, 1981). However, the arrangement of the teeth does not seem to occur in the same form in other vespids (cf. Evans, 1987, for summary), and so this may actually be derived.

Behavior

Use of behavioral characters is somewhat hampered by lack of sufficient detail in published reports, but thanks to the efforts of Hansell, Turillazzi, Ohgushi, and other workers something is now known for all of the genera. Although necessarily tentative, because of the relatively few published accounts, some inferences concerning the evolution of behavioral traits may be drawn. Most of the characters discussed here are placed in a cladistic context for the first time. The emphasis is on reconstruction of groundplan conditions consistent with parsimony, based on optimization (Farris, 1970) of behavioral characters on the cladograms (Figs. 1 and 2). Certain characters which show relationship to other subfamilies are also treated above.

27. Nest material. The use of soil in the construction of nests is clearly more primitive than the use of material of plant origin in the solitary vespids, where only a few species use the latter in a derived type of nest (cf. Carpenter and Cumming, 1985). But this is probably not the case in the social wasps. Polistinae + Vespinae employ plant material; only a few species of *Polybia* use mud (Richards, 1978). The situation is unclear in Stenogastrinae, because both materials are employed in several genera. Soil is used in the one species of *Stenogaster* reported (*S. concinna,* Spradbery, 1975), at least three species of *Liostenogaster* (*L. varipicta,* Williams, 1919; *L. flavolineata,* Pagden, 1958; *L. nitidipennis,* Iwata, 1967; unidentified species, Pagden, 1958; Iwata, 1967; Yoshikawa et al., 1969; Ohgushi et al., 1983b, c, 1985, 1986), and one species of *Anischnogaster* (*A. iridipennis,* van der Vecht, 1972). Plant material alone is employed in the other genera (summary in Iwata, 1976; *Holischnogaster* reported by Hansell, 1986b), as well as species of *Liostenogaster* (unidentified species, Pagden, 1958, Ohgushi et al., 1983b, c) and one species of *Anischnogaster* (*A. laticeps,*

van der Vecht, 1972). Some species have been reported to include both in the same nest (Pagden, 1958; Ohgushi et al., 1983b, c) or to use one or the other type of material (*Parischnogaster mellyi*, Ohgushi et al., 1983b, c). Given this variation, the polarity of this character within the subfamily is difficult to assess, and under any interpretation there is considerable convergent evolution. Because the sister-group of this subfamily uses plant material, one might be inclined to treat this as the groundplan condition in hover wasps as well, and hence another synapomorphy of the social wasps. However, Hansell (1985) has shown considerable differences between the paper made in Stenogastrinae and Polistinae + Vespinae, so the hover wasps are perhaps primitive relative to other social wasps even if use of paper is a synapomorphy of the three subfamilies.

28. Nest architecture. As noted above, the construction of nests entirely from gathered material and which project freely from the substrate is a synapomorphy of the social wasps. Stenogastrinae differ from the other two social subfamiles in not beginning the nest with a petiolate cell (Yoshikawa et al., 1969; van der Vecht, 1977b); this msut be primitive. Few generalizations can be made beyond this, for within the subfamily there is extreme diversity in nest architecture and substrate selection. This has been documented by Williams (1919), Pagden (1958), Iwata (1967), Yoshikawa et al. (1969), Ohgushi et al. (1983b, c, 1985, 1986) and Ohgushi and Salmah (1986). Although specific differences in nest architecture may be relatively constant and have been used in the recognition of new taxa (Sakagami in Yoshikawa et al., 1969; Sakagami and Yoshikawa, 1968), the architecture may be radically different within species, depending on attachment (Iwata, 1967; Hansell, 1981). Iwata (1967, 1976) divided the myriad shapes into two basic types, those with combs of cells and those where the cells are arranged in vertical series. Features common to the two types included cells cylindrical in shape and with their entrances oriented vertically downward. The presence of combs must be inferred as the primitive condition in the subfamily, since it occurs in other social wasps and all genera of hover wasps except *Metischnogaster,* even in astelocyttarus nests. The cells may be rather scattered in a species of *Liostenogaster* and one of *Parischnogaster* which build the nest directly on the substrate, but this cannot parsimoniously be considered as primitive. The arrangement in vertical series is found in *Parischnogaster* and *Metischnogaster* (cf. figs. in Pagden, 1962; Yoshikawa et al., 1969; Ohgushi et al., 1983c), but the form varies within *Parischnogaster,* with comblike arrangements common in *P. mellyi* (cf. pl. II, fig. 1f of Vol. 2 of Saussure, 1852–1858). Hansell (1981) showed that this species was capable of building a range of designs, including linear arrangements, and other species construct "intermediate" nests of elongated combs (figs. in Iwata, 1967; Yoshikawa et al., 1969; Ohgushi et al., 1983c; Ohgushi and Yamane, 1983). *Holischnogaster* also builds an elongate, excentrically attached comb (Hansell, 1986b), and *Anischnogaster* nests encompass a similar range of variation, with a vertical series occurring in one species (van der Vecht, 1972: figs. 57–60). Nests of *Stenogaster* and *Eustenogaster* are different in that they are basically campanulate in form (cf. Pagden, 1958: figs. 4–9 with Spradbery, 1975: figs. 1–3). This latter design may be synapomorphic in these two genera, and elongated combs may similarly characterize *Anischnogaster* + (*Metischnogaster* + (*Holischnogaster* + *Parischnogaster*)), but the evolution of linear series within the latter group must entail some convergence. Hansell (1981) applied Jeanne's (1975) suggestion that elongate linear nests are ad-

aptations for concealment from visual predators. For stenogastrines these would be vespines, but if so this "adaptation" has not been shown to be generally successful (cf. Williams, 1919; Hansell, 1982a; Turillazzi, 1985a for documentation of hornet predation on linear nests). In any event, the interpretation proposed here leaves open the question of whether the irregular comb characterizing *Liostenogaster* (in a general way) is primitive.

Pagden (1958) divided the Malayan species into three groups based in large part on nest architecture, corresponding to the genera *Eustenogaster, Liostenogaster* and *Parischnogaster; Metischnogaster* was possibly a fourth group. This scheme was elaborated by Ohgushi et al. (1983b: fig. I–4) into a detailed evolutionary scenario of nest architecture. The nest architecture of a putative species of *Liostenogaster* was treated as primitive, and adaptive changes from this were hypothesized to have been brought about by predation pressure. This led to the conclusion that where the nest architecture did not show comb formation it was secondary. This scenario shows general congruence to the present analysis, although the reservation must be expressed that simply because *Liostenogaster* is relatively plesiomorph in Figure 2, that does not mean that all of its traits are primitive. Ohgushi et al. also subdivided *Parischnogaster* into three species groups (*striatula, mellyi* and *jacobsoni*) and suggested transitions between architecture types among these groups. Evaluation of that aspect of their scenario must await phylogenetic analysis of the species of *Parischnogaster*.

29. Ant guards. The possible influence of predation on the evolution of nest shape was previously mentioned. Other specific features of nests may be attributed to protection from cursorial predators, namely ants. The disc-like structures on the supports of nests in several species, known as "ant guards," were suggested to provide protection from ants by Williams (1919). They are of two dissimilar types. Structures made of the same material as the rest of the nest are found in species of *Parischnogaster* and *Metischnogaster* (Pagden, 1958, 1962; C. K. Starr, pers. comm.). Secreted structures are found in other species of *Parischnogaster* (Turillazzi and Pardi, 1981; C. K. Starr, pers. comm.), as well as *Eustenogaster* (Pagden, 1958; fig. 8; C. K. Starr, pers. comm.) and possibly *Stenogaster fulgipennis* (van der Vecht, 1975). Turillazzi and Pardi (1981) confirmed that the ant guard material of *Parischnogaster nigricans serrei* repels a few species of ants, and that the material is secreted, at least for the most part, from the abdomen. However, the repellent effect was not universal. It appears that the different types of structures have arisen *de novo* on several occasions within the subfamily. Other forms of protection from ants found in other social wasps, such as the application of oral secretions and rubbing of the nest petiole with the terminal metasomal sterna (behavior patterns 8 and 9 of Sakagami and Yamane 1983: table I–2), evidently have no counterpart in stenogastrines. In that respect hover wasps are relatively primitive.

30. Envelope. Stenogastrine nests are typically gymnodomous, as is also true of nests of primitive paper wasps. However, nests of *Eustenogaster* are enclosed by an envelope. As pointed out by Iwata (1967), in most species the envelope is merely an elaboration of the outer walls of the peripheral cells, for which the term "pseudenvelope" has been used (Yoshikawa et al.,1969). Something approaching this is seen in a *Liostenogaster* species (Yoshikawa et al., 1969: figs. 5–6). However, in *E. calyptodoma* there is an envelope constructed independently of the comb, as is the case in higher social wasps. This last is clearly convergent, as it is within higher social

wasps; Polistinae do not primitively construct an envelope. Construction of an envelope is an autapomorphy of *Eustenogaster,* with the independent envelope found in *E. calyptodoma* perhaps derived from the "pseudenvelope" found in other species of the genus.

31. Oviposition. Oviposition behavior in Stenogastrinae has been described by Pardi and Turillazzi (1981), Hansell (1982a), Turillazzi and Pardi (1982), Sakagami and Yamane (1983) and Turillazzi (1985e). It is an indirect process. After placing a droplet of secretion from the metasoma in the mouthparts (not in the cell as stated by previous authors; Turillazzi, 1985e), the egg is extruded, grasped by adhering to the secretion in the mouthparts, and deposited in the cell. Further secretions from the metasoma are then placed upon the egg. As emphasized by all of these authors, this behavior is unique in the Vespidae. It is an autapomorphy, hence completely uninformative on relationships, and hence of no use whatsoever in analysis of interrelationships of Stenogastrinae and other vespid subfamilies, contrary to Sakagami and Yamane (1983) and Turillazzi (1985e).

32. Provisioning. As discussed previously, the provisioning of cells in Stenogastrinae shows derived similarity with Polistinae + Vespinae. It is simultaneous and progressive, and consists of a masticated arthropod paste. To the extent that sufficient food is provided for a day or more (Spradbery, 1975), hover wasps are primitive relative to other social wasps, and so "intermediate." The actual hunting itself was first described by Williams (1928). It involves hovering by the wasp at a spider's web and plucking of small prey from the web. This is characteristic and unique, hence an autapomorphy of the subfamily. Related issues are whether food is provided before egg hatch, and to what extent it is endogenous (of glandular origin). Spradbery (1975) and Sakagami and Yamane (1983) have considered provision before egg hatch to be a primitive feature similar to the state found in Eumeninae, and the latter authors argued that it showed phylogenetic relationship to Eumeninae, which is obviously a misinterpretation based on symplesiomorphy. But the whole character may be questioned. As discussed above under oviposition, what is provided before egg hatch is primarily a substance of glandular origin which may not have a trophic function (Hansell, 1982a; Turillazzi, 1985d). To the extent that prey items are ever provided prior to egg hatch (one species, Turillazzi, 1985d), they are malaxated or very small and incorporated into the secretion. The secretion has not been observed to have been consumed, and may instead serve a variety of other functions, including that of a platform for food (Turillazzi, 1985d). The use of the substance in itself is autapomorphic for the subfamily, as noted above. If in fact it does not have a trophic function, then stenogastrines show derived similarity to other social wasps in also not provisioning until after egg hatch.

33. Trophallaxis. Spradbery (1975) listed larval-adult trophallaxis as "probably not" occurring in Stenogastrinae, which is another symplesiomorphy with Eumeninae and so not informative on relationships. However, there is some doubt that this behavior is absent in Stenogastrinae (Turillazzi and Pardi, 1982; Turillazzi, 1985b, 1986a). It should be studied further; if the behavior is confirmed in hover wasps it might be another synapomorphy with other social wasps, although the behavior patterns would be rather different. Be that as it may, another form of trophallaxis, that between adults, probably is a synapomorphy of the social wasps. It has been reported in numerous studies of Stenogastrinae (Williams, 1928; Pagden, 1962; Tu-

rillazzi and Pardi, 1982; Hansell, 1983, 1987; Sakagami and Yamane, 1983; Turillazzi, 1985a, b, 1986b) and should be looked for in other species in order to assess its generality. It does not occur in solitary vespids, but is well known in other social vespids, and Pardi and Turillazzi (1982) cited it as a similarity between these three subfamilies, but then attributed it to convergence. As indicated by the results of Carpenter (1981) and in the section on subfamily placement, there is no evidence that the view of convergence is correct.

34. Thermoregulation. Rare wing fanning is the only putative thermoregulatory behavior known to occur in hover wasps (Williams, 1919; Sakagami and Yamane, 1983). Absence of such highly derived behaviors as transport of water droplets is simply primitive, but wing fanning, if general and indeed thermoregulatory, could be another derived similarity with other social wasps.

35. Extraction of meconium. This is part of the extended care, into the pupal stage of these wasps. First suggested by Spradbery (1975) for *Stenogaster concinna,* it has since been observed in other stenogastrines (Turillazzi and Pardi, 1981; Sakagami and Yamane, 1983; Turillazzi, 1986b). The meconium is extracted through the entrance to the cell. In those paper wasps which extract the meconium, it is done through the bottom of the cell (Jeanne, 1980) or after adult eclosion. This extraction behavior, if shown to be general in the subfamily, would be another autapomorphy. Turillazzi (1985b) suggested that the meconium is removed either for hygenic reasons or to facilitate the emergence of the adult, or both.

36. Closure. Sealing of the rearing cell "rarely" by the female in Stenogastrinae was a feature mentioned by Spradbery (1975); in Eumeninae the female always seals the cell (this is also true of other solitary vespids) but in higher social wasps the female does not do so. Sealing of the rearing cell is actually more common in the subfamily than stated by Spradbery. Complete sealing has been reported in *Liostenogaster varipicta* (Williams, 1919), *L. nitidipennis* (Iwata, 1967), *Anischnogaster iridipennis* (van der Vecht, 1972), *Parischnogaster timida* (Williams, 1919), *P. mellyi* (Iwata, 1967; Hansell, 1981), *P. nigricans serrei* (Iwata, 1967; Pardi and Turillazzi, 1981), and *Holischnogaster gracilipes* (Hansell, 1986b). Partial sealing of the rearing cell, which is no more than narrowing of the entrance, has been observed in *Parischnogaster depressigaster* (Williams, 1919), *P. striatula* (Iwata, 1967), *P. alternata* (Turillazzi, 1986b), *Eustenogaster calyptodoma* (Sakagami and Yoshikawa, 1968) and *E. eximia* (Krombein, 1976). Only *Stenogaster concinna* has been reported to provide no form of cell closure (Spradbery, 1975). The ground-plan state of Stenogastrinae is thus parsimoniously inferred to be sealing of the cell, given the cladogram of Figure 2. As such it is a symplesiomorphy, and so uninformative on subfamily relationships. Loss of this trait is perhaps another shared derived similarity between *Eustenogaster* and *Stenogaster,* but if so there is convergence in some species of *Parischnogaster.*

37. Cocoon. Spradbery (1975) noted that in Stenogastrinae the pupal cocoon was not complete, whereas in the other subfamilies he listed it was. *Parischnogaster depressigaster* (Williams, 1919), *Eustenogaster calyptodoma* (Sakagami and Yoshikawa, 1968), and *E. eximia* (Krombein, 1976) have been reported to line the cell wall with silk but not to have a complete cocoon. Other species appear to lack a cocoon entirely. An incomplete cocoon then, is the groundplan condition in the subfamily, an autapomorphy, and hence uninformative on subfamily relationships. It may be added that the suggestion of Iwata (1976) that sealing of the rearing cell

occurs because there is no cocoon spun is illogical; the first trait is primitive and the second is derived, and so they cannot be causally related.

38. Nest sharing. As discussed previously, on present evidence nest sharing is parsimoniously inferred to be a synapomorphy of the three social wasp subfamilies. It may characterize the colony cycle in all species of hover wasps, but is possibly only facultative; long-term observation on many species is required to establish this. Colony foundation is by single foundresses in Stenogastrinae, although absconding swarms (West-Eberhard, 1982) have been observed (Turillazzi, 1985a). Recruitment usually occurs by addition of daughters (Krombein, 1976; Turillazzi, 1982, 1985a; Hansell, 1983, 1987; Yamane et al., 1983a; inferred by van der Vecht, 1972, and Spradbery, 1975).. Recruitment by joining has also been reported in *Liostenogaster flavolineata* (Hansell et al., 1982), *P. nigricans serrei* (Turillazzi, 1982, 1985a), *P. mellyi* (Hansell, 1983; Sakagami and Yamane, 1983), and *P. alternata* (Turillazzi, 1985c). Joining typically occurs prior to the emergence of brood and is frequently accompanied by usurpation or is short-term (Turillazzi, 1982, 1985a; Hansell, 1983, 1987; Sakagami and Yamane, 1983; Yamane et al., 1983a). Joining may occur later in the colony cycle (Yamane et al., 1983a) or persist for a relatively extended time (Turillazzi, 1985c, 1986a, b) but seems to me qualitatively similar in all these cases, contrary to Turillazzi (1985c, 1986a, b). An apparently different phenomenon is the internidal drifting first reported for *P. striatula* (Yoshikawa et al., 1969). In a small aggregation of very closely spaced colonies they observed frequent movement of marked females among several nests. However, Hansell (1982b) repeated this study and did not find frequent interchange, but instead active nest defense against conspecifics. Females only succeeded in landing on foreign nests when no resident was there and then attacked the brood. As Hansell pointed out, the data published by Yoshikawa et al. (1969) do not indicate whether females landed on nests in the presence of a resident. Similar comments apply to the internidal drifting reported in *P. mellyi* by Yamane et al. (1983a, b). The interchange apparently occurred on abandoned or usurped nests, which would accord with the observations of Hansell (1981, 1983) of typical active nest defense in this species. Remarkably, Yamane et al. (1983a, b) stated that reoccupants and usurpers continued to rear the brood of the previous occupant, although they also stated (1983a:21) "it is uncertain whether there occurred any selective eating or elimination by new occupants." Hansell (1987) has reported similar rearing of brood by usurpers in *Eustenogaster calyptodoma,* and suggested that acquisition of a brood is advantageous in providing (eventual) foraging assistance. Frequent interchange among closely spaced colonies may thus be usurpation attempts, and joining explicable if average relatedness was high or mutual care of the nest occurred—and moving females had a sufficient chance of reproduction on the new nests (Yamane et al., 1983a). Shifts between (young) nests are well known in *Polistes* (West-Eberhard, 1969; Kasuya, 1981; Itô, 1984) and are generally considered to be among closely related individuals (e.g., Ross and Gamboa, 1981).

Cell re-use during a single colony cycle may also be general in the subfamily; it is usually noted in long-term studies (nest re-use has also been reported: Yamane et al., 1983a; Turillazzi, 1985a). If cell re-use is general, it is another synapomorphy with other social wasps.

39. Division of labor. Cooperative brood care was reported in *Parischnogaster depressigaster* and *Liostenogaster varipicta* by Williams (1919) in the first behavioral

study of hover wasps. It has since been observed in every long-term study. Division of labor has also been observed. A linear dominance hierarchy has been reported in *Parischnogaster* sp. (Yoshikawa et al., 1969) and *P. nigricans serrei* (Pardi and Turillazzi, 1981; Turillizzi and Pardi, 1982). A three-level dominance hierarchy has been observed in *Liostenogaster flavolineata* (Hansell et al., 1982). Position in the hierarchy is correlated with ovarian development. Division of labor occurs in *P. mellyi* (Hansell, 1983; Yamane et al., 1983a, b), *Holischnogaster gracilipes* (Hansell, 1986a), *Eustenogaster eximia* (Krombein, 1976) and *E. calyptodoma* (Hansell, 1987), but clear dominance hierarchies have not been identified. Rather, certain individuals spent more time on the nest while others spent more time foraging, and this was correlated with ovarian development. The workerlike individuals may be daughters of the foundress (Krombein, 1976; Yamane et al., 1983a; Hansell, 1987). All females may eventually mate (Turillazzi, 1985a, 1986a, Hansell, 1987), subordinates are presumed to lay eggs (Hansell, 1983), and subordinates have been observed to become foundresses (Turillazzi, 1982; Yamane et al., 1983a, b) or come to dominate (Hansell et al., 1982). Turillazzi and Pardi (1982) reported statistical size differences correlated with fertilization in *P. nigricans serrei,* but Turillazzi (1985a) did not find any in the same species. Similar variation in the statistical differences reported by Richards and Richards (1951) for some paper wasp species has been observed (Carpenter and Ross, 1984). Therefore morphological castes apparently do not exist in Stenogastrinae. Instead, these reports indicate that the reproductive division of labor is behavioral— and temporal. Workerlike behavior may be an alternative reproductive strategy (West-Eberhard, 1981) whose expression is facultative (West-Eberhard, 1987) and often temporary.

All of these species are at stage III, the "rudimentary-caste-containing stage," of West-Eberhard's (1978) model for the origin of social behavior in wasps, as realized by Hansell (1983) and Turillazzi (1985a). The question is then whether temporary division of labor also characterizes all those species where nest sharing occurs in smaller colonies or persists over a relatively shorter part of the colony cycle. It was not observed in *Stenogaster concinna* by Spradbery (1975), but he apparently did not make detailed observations on the multi-female nests he found. It has been reported in the small, short-term colonies of *Eustenogaster* (Krombein, 1976; Hansell, 1987), where daughters assist their mothers in brood care. Critical study of other species, particularly in these two genera and *Anischnogaster,* is required to establish the generality of temporary division of labor, but it may occur in all stenogastrine species. If this is true it is another synapomorphy of all social wasps, rather than just Polistinae + Vespinae (Carpenter, 1981). This would have two major implications. First, the groundplan condition in Stenogastrinae would then differ little from the ancestral condition in Polistinae—only in the presence of permanent sterility in the latter group. And here it should be recalled that the workers in the primitive paper wasp genera are at least initially "hopeful" reproductives (West-Eberhard, 1978) and worker behavior thus in a sense conditional (West-Eberhard, 1981). Mechanisms for queen control (monopolization of oviposition, West-Eberhard, 1987) are better developed in Polistinae than Stenogastrinae. Second, the distinction between West-Eberhard's (1978) "primitively social stage (II)" (casteless nest sharing) and "rudimentary-caste-containing stage (III)" is then not exemplified in the social Vespidae

clade, and so the distinction has perhaps not been important in the evolution of this group.

40. Male behavior. The mating systems of very few hover wasps have been studied. Primarily unisexual aggregations away from nests—"male clubs" (Hansell, 1986a) have been reported in *Eustenogaster luzonensis* (Williams, 1919), *Stenogaster concinna* and *Anischnogaster iridipennis* (Spradbery, 1975), *Parischnogaster mellyi* (Turillazzi, 1983a), and *Holischnogaster gracilipes* (Hansell, 1986a). It is unknown whether this behavior functions in reproduction. Patrolling and displaying behavior away from nests has been observed in *Metischnogaster* (Pagden, 1958, 1962), *Parischnogaster nigricans serrei* and *mellyi* (Turillazzi, 1982, 1983a, b), and *Liostenogaster* (Turillazzi, 1986a); marking of perches occurs in the latter. Switching between aggregations and patrolling at particular times of day occurs in *P. mellyi* (Turillazzi, 1983a). Male behavior is quite diverse in Eumeninae (cf. Smith and Alcock, 1980), and although patrolling is common in Polistinae, it is not in *Polistes* (cf. Jeanne and Castellón Bermúdez, 1980). Patrolling in loose aggregations is typical in Vespinae (e.g., Post, 1980), although sibling mating on the natal nest may be common (e.g., Akre et al., 1982). Given the few data on hover wasps and this diversity in the outgroups, it does not seem possible to specify the direction of evolutionary change at this time.

<div align="center">RESULTS</div>

The cladogram for the characters coded in Table 2 is shown in Figure 2. The length of the cladogram is 16. The consistency index (the sum of the states of all the characters, divided by the length of the tree; Kluge and Farris, 1969) is 0.875. The matrix of Table 2 includes three autapomorphic states; when these are deleted the length of the cladogram is 13, with a consistency index of 0.846. The characters are highly congruent; only two extra steps are required. These are in character 5, the number of male mandibular teeth, and character 16, the propodeal sculpture. Convergence is thus inferred for both of these characters. The other characters listed in Table 2 support the cladogram quite strongly. The diagnosis of the cladogram (Farris, 1979) for all of the characters discussed in this paper follows: the synapomorphies of each grouping of genera and autapomorphies of each genus are summarized. Apomorphic groundplan features of the subfamily as a whole are also listed.

STENOGASTRINAE

Autapomorphies not discussed by Carpenter (1981) include: character 1, forewing second submarginal cell rectangular; 6, labial palpus with first segment greater than or approximately equal to the combined length of segments 2–4; 10, pronotal and pretegular carinae lost; 21, male sternum VII flattened; 25, larva with antennal papilla; 26, larval mandible with one tooth set back from margin; 31, indirect oviposition; 32, hunting behavior and use of endogenous substance as food platform; 35, meconium extraction; 36, pupal cocoon incomplete. The following apomorphic behavioral characters are interpreted as synapomorphies with Polistinae + Vespinae: 27, nests constructed with plant material (?); 28, nests free hanging; 32, simultaneous progressive provisioning with masticated arthropod paste, after egg hatch (latter

Table 2. Character codings for each genus.

Genus										
Liostenogaster	SMOOTH	NORMAL	GAP	SPINOSE	POINT	NORMAL	THREE	EQUAL	NORMAL	ROUND
Parischnogaster	STRIATE	PETIOLE	FUSED	FLAT	POINT	DILATED	THREE	EQUAL	CLUB	NARROW
Holischnogaster	STRIATE	PETIOLE	FUSED	FLAT	POINT	DILATED	THREE	EQUAL	CLUB	NARROW
Metischnogaster	STRIATE	PETIOLE	FUSED	SPINOSE	POINT	DILATED	TWO	EQUAL	FLAT	NARROW
Anischnogaster	PUNCTATE	PETIOLE	FUSED	SPINOSE	POINT	NORMAL	THREE	EQUAL	NORMAL	ROUND
Stenogaster	STRIATE	NORMAL	FUSED	SPINOSE	ROUND	NORMAL	ONE	GREATER	TIPPED	ROUND
Eustenogaster	SMOOTH	NORMAL	FUSED	SPINOSE	ROUND	NORMAL	ONE	GREATER	NORMAL	ROUND

aspect only probable); 33, adult trophallaxis, possibly also larval-adult trophallaxis; 34, thermoregulation by wing fanning (?); 38, nest sharing and cell re-use; 39, cooperative brood care and temporal division of labor (probable). The groundplan condition of character 40, male behavior, is unclear.

Liostenogaster

The only autapomorphy of this genus is character 16, propodeum smooth, which is convergent in *Eustenogaster*.

(Eustenogaster + Stenogaster) + (Anischnogaster + (Metischnogaster + (Holischnogaster + Parischnogaster)))

The grouping of all hover wasp genera aside from *Liostenogaster* is supported by character 3, fusion of the occipital carina with the hypostomal carina.

Eustenogaster + Stenogaster

A sister-group relationship between these two genera is supported by three morphological characters: 4, male clypeus rounded ventrally; 5, male mandibular teeth reduced to one; and 7, maxillary palpus with the length of segment 2 greater than the combined length of segments 3–6. Two behavioral features may also support this relationship: 28, nests campanulate in shape; and possibly 36, cells not completely closed by female. Character 6, first segment of labial palpus relatively longer than in other hover wasps, may also be a shared derived feature of these genera.

Eustenogaster

Autapomorphies of the genus include: 2, pigmented posterobasal area in male hindwing; 13, scutellum strongly carinate; 16, propodeum smooth (convergent in *Liostenogaster*); 30, nest with "pseudenvelope."

Stenogaster

The monophyly of this genus is shown by characters 8, male antenna with apical flagellomere modified; 15, raised lamella above propodeal orifice; 23, volsella with cuspis + lamina strongly narrowed medially.

Anischnogaster + (Metischnogaster + (Holischnogaster + Parischnogaster))

The grouping of these four genera is supported by character 20, development of a petiole on metasomal segment II. Character 28, nest with comb elongated, may also support this component.

Anischnogaster

The monophyly of this genus is weakly established by character 5, male mandible with proximal teeth blunted; and 16, propodeum punctate (polarity unclear).

Metischnogaster + (*Holischnogaster* + *Parischnogaster*)

The grouping of these three genera is supported by character 14, narrowing of the propodeal valvula posteriorly; and 24, aedeagus apically compressed and dilated in lateral view.

Metischnogaster

The monophyly of *Metischnogaster* is shown by a large suite of features, including characters 2, hindwing with posterior fringe of hairs greatly elongated; 5, male mandible bidentate; 8, male antenna with flagellomeres flattened; 9, vertex with median longitudinal groove; 11, notauli strongly impressed; 12, male pleural area sunken, densely pubescent, and bordered posteriorly by carina; 14, propodeal valvula essentially lost; 17, male foretibia with spatulate setae; 19, spiracles of metasomal segment II visible in dorsal view; 24, aedeagus with subapical lateral projections; 29, nest with ant guards.

Holischnogaster + *Parischnogaster*

A sister-group relationship between these two genera is established by two features: 8, distally swollen antennae; and 22, male parameral spine flattened and greatly enlarged.

Holischnogaster

This genus is certainly monophyletic, since it is monotypic. However, it does not have any autapomorphies among the characters discussed in this paper. Of the two features by which it was distinguished from *Parischnogaster* in the original description (van der Vecht, 1977a), male midtarsi symmetrical and mouthparts elongate, it has the plesiomorphic state in the first and possibly the second as well (see above). As discussed below, recognition of a separate genus for this species seems unjustified.

Parischnogaster

The monophyly of this genus is shown by character 18, male midtarsi asymmetrical. The mouthparts of *Parischnogaster,* specifically the palpi, tend to be shorter than in its sister-group, but there is variation within the genus (as well as among other stenogastrines), and in my view the differences between the two genera are not significant.

DISCUSSION

The implications of the results of this analysis are of three sorts. The first is taxonomic. All of the previously recognized genera are monophyletic—but that does not mean that recognition of all of them is well justified. *Holischnogaster* is differentiated from its sister-group *Parischnogaster* primarily by plesiomorphy in one character. Although a sister-group relationship is thereby formally recognized, little is gained in the process of efficient description of character data (diagnostic efficiency of Farris, 1979) which is the purpose of classification. Recognition of *Holischnogaster* itself contributes nothing to this process, and separation of *Parischnogaster* contrib-

utes only one character, male midtarsi, which varies within other vespid genera. By contrast, one of the characters establishing this sister-group relationship, parameral spine dilated, is an outstanding feature, unique in the entire family. Van der Vecht (1977a:73) separated *Holischnogaster* as a genus because "there may be important differences in behaviour with regard to feeding and mating." No differences have yet been shown, and in any event the similarity in the male genitalia seems far more "important" as a genus character. The recognition of two genera in this case is just the sort of oversplitting which has rendered the classification of other vespid subfamilies chaotic, with an inflexible, confusing nomenclature and little discernible benefit (cf. Carpenter and Cumming, 1985; Carpenter, 1986, 1987). As I have done in Vespinae (Carpenter, 1987), I am resisting this trend here. *Holischnogaster* is herewith synonymized with *Parischnogaster* (NEW SYNONYMY).

The second implication of the results concerns biogeography. The Stenogastrinae are endemic to the Indo-Pacific, ranging from the Indian subcontinent and Sri Lanka to New Guinea. Two genera, *Stenogaster* and *Anischnogaster,* are endemic to New Guinea and neighboring islands (Waigeo, Misool, Aru, Yapen; cf. van der Vecht, 1972, 1975). This type of distribution has been termed Papuan (e.g., Gressitt, 1956), and was classically considered to be a part of the Australian region (Wallace, 1860). The other genera do not occur any further east than Mindanao and Sulawesi (cf. Schulthess, 1927). Thus, their distribution is in the classical Oriental Region (Wallace, 1860). Replacing the taxa in Figure 2 with these areas, it is seen that the transition between the Papuan and Oriental Regions is replicated. This division corresponds to Wallace's famous line, and it might be thought that this accords with the classical treatment. However, two-area statements are basically uninformative in historical biogeography; the interesting question is what are the relationships of these two areas to a third. One potentially fruitful approach to this problem will be the study of the interrelationships of the species inhabiting the Oriental "region." Schuh and Stonedahl (1986) cite evidence from several groups which shows that part of the Oriental "region" is more closely related to the Papuan "region" than to other parts of the Oriental "region." The same pattern may occur within the Oriental hover wasp genera.

Finally, there are various implications of this analysis for the evolutionary study of behavior. As discussed above, there is considerable evidence from behavioral data to support the close relationship of Stenogastrinae to Polistinae + Vespinae. The characters in the subfamily tables of Spradbery (1975) and Sakagami and Yamane (1983) show similarity in derived features between these groups. The characters where stenogastrines lack the derived states of other social wasps are either primitive absences or unique derived features in Stenogastrinae. There are thus no grounds for attributing similarity in the basic (groundplan) behavioral patterns in stenogastrines and other social wasps to convergence. Instead, such similarities must be inferred to be the product of descent from a common ancestor.

As the discussion of various aspects of social behavior shows, the hover wasps as a whole may not be very different in these aspects from the relatively primitive Polistinae. Stenogastrinae may primitively be at the rudimentary-caste-containing stage (III) of West-Eberhard's (1978) model for the origin of social behavior in wasps. This would indicate that the common ancestor of all social wasps attained this condition before diversifying, and so that the transition between West-Eberhard's

stage II (casteless nest sharing) is not exemplified within any subfamily—or that the distinction is not significant in Vespidae. However, the fundamental tenet of West Eberhard's model, that the evolution of eusociality occurred in polygynous family groups, is still corroborated by this inferred common ancestor. The basic (ancestral) differences between the social behavior in stenogastrines and that of the higher social wasps may then turn out to be: 1) dominance is more strongly enforced in the latter group (i.e., mechanisms of queen control are better), and 2) colonies are also larger. Dominance hierarchies have evolved convergently within Stenogastrinae and other social wasps, and doubtless other features of social behavior as well, but apparently eusociality as such is not convergent—although that term is applied in this case to a temporal, facultative phenomenon (a "serial polygyny"). The larger colonies of Polistinae + Vespinae have been attributed to beginning the nest with a petiolate cell (van der Vecht, 1977b), which Hansell (1985) speculated led to the selection of tough paper, thus permitting evolution of large nests. Is this relatively simple trait then the crucial difference between the hover wasp lineage with some 67 species (van der Vecht, 1977a), rather uniform in morphology, behavior and ecology, and the paper wasp–hornet lineage with over 800 highly diverse species?

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APPENDIX

List of taxa examined. N.C. indicates new combination. * indicates that the male genitalia were dissected.

Liostenogaster
  flavolineata (Cameron)
  nitidipennis (Saussure)*
  varipicta (Rohwer), N.C.*
  1 new species*

Stenogaster
  adusta Vecht*
  concinna Vecht*
  macilenta Vecht
Eustenogaster agilis (Smith), N.C.*

calyptodoma (Sakagami & Yoshikawa)*
eximia (Bingham)*
fulvipennis (Cameron), N.C.*
hauxwellii (Bingham)*
luzonensis (Rohwer), N.C.*
micans (Saussure)*
scitula (Bingham)*
3 new speices
Anischnogaster
dubia Vecht*
iridipennis (Smith)*
loriai maculata Vecht*
spilaspis (Cameron)*

Metischnogaster
cilipennis (Smith)*
drewseni (Saussure)*
Parischnogaster
depressigaster (Rohwer)*
gracilipes (Vecht), N.C.*
jacobsoni (Buysson)*
mellyi (Saussure)*
nigricans (Cameron)*
striatula (Buysson)
timida (Williams)

REVISION OF *TACHIONA* SHARP
(COLEOPTERA: STAPHYLINIDAE: ALEOCHARINAE)
WITH A DESCRIPTION OF THE LARVA OF *T. LATIPENNIS,*
NEW SPECIES, AND A PRELIMINARY ASSESSMENT
OF GENERIC RELATIONSHIPS

James S. Ashe[1] and Q. D. Wheeler[2]

Abstract. —The aleocharine genus *Tachiona* Sharp and the single previously described species *T. deplanata* Sharp from Mexico are redescribed. A lectotype is designated for *T. deplanata* from the syntype series. Two new species, *T. nitida* Ashe and *T. latipennis* Ashe, are described from material collected in Mexico and Panama respectively. A key is provided for separation of the known species of *Tachiona*. Larvae collected in association with adults of *T. latipennis* from the interior of a web covering a tree wound were presumed to be conspecific with them, described, and compared with larvae collected with a female of *T. nitida* from a similar web-covered tree hole. Illustrations of diagnostic features of adults and larvae are provided. Based on mouthpart structure, particularly the styliform labial palpi and elongated maxillary lobes, *Tachiona* is shown to be a member of the probably monophyletic bolitocharine subtribe Silusina. Within the Silusina, members of *Tachiona* are very similar to those of *Diestota* Mulsant and Rey in a number of characteristics, especially form of the spermatheca and aedeagus. More precise analysis of relationships among the Silusina must await a more detailed survey of structural features among included taxa.

In 1978, while collecting in Panama, one of us (Wheeler) discovered a number of curious aleocharine staphylinids and associated larvae on the inside of an unusual web mixed with wood chips covering a two inch diameter hole in a living tree. A number of the adults and larvae were collected and the curious habitat noted and photographed. Later the staphylinids were deposited in the Field Museum of Natural History. When adults were recently examined and compared with determined specimens in the Field Museum, they proved to represent an undescribed species in the very poorly known genus *Tachiona* Sharp. Recently, a specimen of a third species was collected with associated larvae from the inside of a similar web covering a tree hole in Mexico by Dr. J. K. Liebherr and made available to us.

Tachiona was described by Sharp in 1883 based on three female specimens collected in Mexico. From these he described a single species, *T. deplanata.* Except for repetition of Sharp's description by Fenyes (1920), we have been unable to locate any later reference to this genus other than catalog citations (e.g., Bernhauer and Scheerpeltz, 1926). Although members of *Tachiona* are very distinctive in general habitus, the descriptions of both the genus and the single included species are very sketchy and incomplete. Were it not for the habitus drawing of *Tachiona deplanata*

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provided by Sharp (1883, plate 6, fig. 21), it would be virtually impossible to identify specimens of *Tachiona* from available literature.

Discovery of two undescribed species with associated larvae and the fortunate presence of a specimen of the syntype series of *T. deplanata* in the collections of the Field Museum provided us with the opportunity to redescribe the genus and type species, describe the new species and their probable larvae, and discuss the probable taxonomic position and phylogenetic relationships of *Tachiona*.

Tachiona Sharp

Tachiona Sharp, 1883:284–285; Fenyes, 1920:127–128; Bernhauer and Scheerpeltz, 1926:562.

Diagnostic combination. Among aleocharine genera with 4,4,5 tarsal segmentation members of *Tachiona* are easily recognized by the combination of: broad, explanate and flattened body form; slightly to markedly emarginate clypeal margin; styliform labial palpi (Fig. 5); elongate, apically bifid ligula (Fig. 5); elongate galea and lacinia (Fig. 2); markedly transverse pronotum with fully exposed hypomera; pronotal setae directed laterally or slightly latero-caudad from midline; mesocoxae very widely separated by more or less truncate meso- and metasternal processes; the distinctive secondary sexual characteristics; and, the distinctive complexly coiled female spermatheca (Figs. 10, 11).

Description. Moderate sized, length 5.0–6.5 mm. Body shape very broad and explanate in dorsal aspect, markedly dorso-ventrally flattened, abdomen tapered from broad base to moderately pointed apex. Body color reddish-flavate to light reddish-brown with or without darker piceus or blackish markings on head, prothorax, elytra and apical abdominal segments. Body sculpture with head, pronotum and elytra obsoletely reticulate or smooth and abdomen obsoletely reticulate to distinctly transversely reticulate, integument surface strongly shining; integument moderately to sparsely and more or less uniformly pubescent with short and appressed microsetae; macrosetae conspicuous, long and black.

HEAD. Broadly transverse, about 1.5–1.9 times as wide as long; basal angles broadly rounded; covered basally by anterior margin of pronotum; neck absent. Eyes moderate in size, directed anteriorly, greatest width across eyes about equal to width of head at posterior margin of eyes. Margin of clypeus slightly to markedly emarginate medially. Tempora moderately long, about 1.2–1.5 times length of eyes, rounded basally. Infraorbital carina well developed beneath eye and on lateral base of head and complete to maxillary fossae; neck carina well developed to gular sutures. Microsetae fine, uniformly distributed, moderately dense to more or less sparse, appressed to suberect, directed from lateral margins toward midline of head or slightly antero-medially; punctures moderate in size, uniformly distributed. Antenna very short to moderate in length, length equal to head and pronotum together or extended to basal 0.4 of elytra, articles moderately to very compactly arranged, segments slightly to markedly flattened; antennomere IV quadrate to markedly transverse, V quadrate to markedly transverse, 1.0–3.5 times as wide as long, VI–IX transverse, about equal in size and shape or more distal segments slightly wider and more transverse, antennomere X slightly to markedly transverse, about 1.2–2.5 times as wide as long.
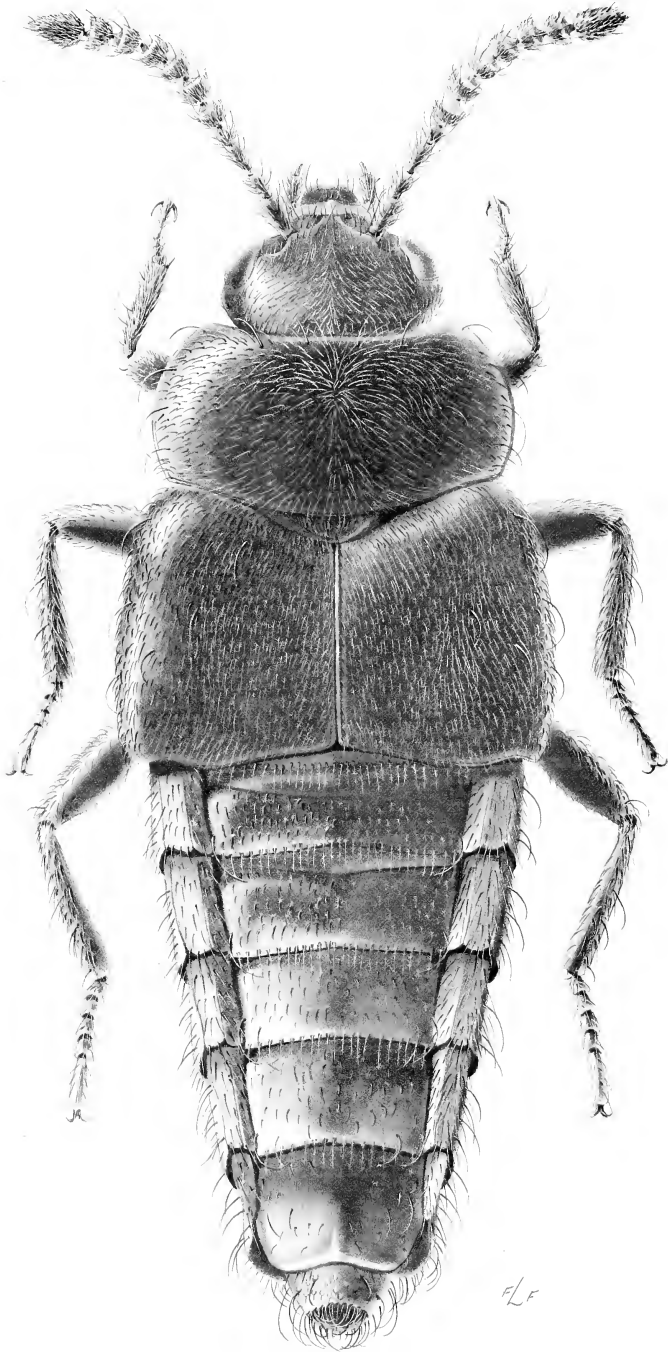
Fig. 1. *Tachiona latipennis* Ashe, habitus.

MOUTHPARTS. Labrum as in Figure 3. Right mandible (Fig. 4) with slight but inconspicuous projection in area of internal tooth, absent from left mandible; mandibular apices acute, entire; molar region with numerous small teeth in transverse rows; prostheca with flattened, apically emarginate structures medially. Maxilla (Fig. 2) with galea and lacinia elongate, about equal in length; galea more robust than lacinia, apex densely pubescent with long filiform setae; lacinia elongate, slender, more or less acutely pointed, internal surface with comb of single row of well separated spines in apical 0.25 followed more proximally by a small dense patch of setae medially with or without a large, robust spine at the proximal edge, and a distinct row of numerous setae on dorsal surface in proximal 0.7; maxillary palpus 4-articled, without pseudosegment on article IV. Labium (Fig. 5) with palpi 2-articled, styliform, elongate; ligula elongate, slender, about 3.0–3.2 times as long as greatest width, divided into two lobes in apical 0.3, apex of lobes narrowed to short, robust, digitiform projections; medial setae 2, bases more or less contiguous on slight knob or projection; prementum with 5–6 pseudopores in narrow longitudinal row medially, and with 2 large pores, 1 large spinose pore and about 10–15 small pseudopores laterally on each side.

THORAX. Pronotum markedly transverse, about 1.7–2.3 times as wide as long; very flattened in cross section; margin distinctly beaded; antero-lateral angles obtusely rounded and indistinct, posterior angles distinct, sides broadly rounded; widest near middle or in apical third; posterior margin slightly and broadly bisinuate or sinuations absent and base broadly rounded; microsetae numerous to relatively sparse, uniformly distributed, appressed, setae directed laterally or slightly latero-caudad from midline, setae in midline directed posteriorly in posterior 0.6–0.7 and more or less anteriorly in anterior 0.4–0.3; macrosetae conspicuous, long, thin and dark; surface uniformly and moderately punctured, distance between punctures about 1.0 to 2.0 times average width of punctures; integument microsculpture obsoletely reticulate to smooth, surface strongly shining. Hypomera broadly and entirely visible in lateral aspect. Elytra 1.2–1.3 times as long as pronotum; outer apical angles slightly sinuate or sinuations obsolete; microsetae numerous, uniformly distributed, setae directed more or less posteriorly; macrosetae long, thin and dark, three macrosetae on lateral margin especially conspicuous; integument with microsculpture smooth to obsoletely reticulate between punctures, surface strongly shining; surface uniformly and moderately punctured, distance between punctures slightly less than to about 1.3 times average width of punctures. Prosternum transverse, produced medially as a large knob or longitudinal carina. Mesosternum very short in front of coxae, not carinate medially; meso- and metasternal processes very broad, almost contiguous at middle of mesocoxal cavities, mesocoxal cavities very broadly separated; mesosternal process moderate in length, extended to 0.3–0.4 times length of mesocoxal cavities, very broad and truncate apically; metasternal process long, extended to near middle of mesosternal cavities, truncate apically; isthmus very short, broad, in same plane as metasternal process and distinguished from it only by a slight bead which delimits the anterior margin of the metasternal process. Mesosternal process: isthmus: metasternal process ratio about 4:1:5. Metepisternal setae numerous, in 3–4 irregular rows, setose area not delimited by a carina. Legs with tarsal formula 4,4,5; posterior tarsomeres I–IV approximately equal in length and V about as long or slightly longer than II–IV together. Tarsomeres not robust and only slightly flattened laterally to distinctly robust and markedly flattened laterally.

ABDOMEN. General shape broad at base and sides uniformly converging to more or less acutely pointed apex. Terga III–IV slightly to moderately transversely impressed at base. Sterna not impressed. Tergum X quadrate, setal patch quadrate with setae absent postero-medially to produce an inverted, slightly V-shaped setal patch. Integument of abdomen with transverse microsculpture moderately developed or microsculpture obsolete, integument strongly shining.

AEDEAGUS. (Figs. 6, 8, 9) Relatively simple, without complex internal hooks, spines or plates.

SPERMATHECA. (Figs. 10, 11) Complex and doubly coiled, with elongate basal bulb.

SECONDARY SEXUAL CHARACTERISTICS. Male abdominal tergum VII with broad, low medial carina; tergum VIII (Fig. 7) produced as broad truncate lobe, apical margin of lobe with 3–4 small teeth on each half of midline; surface of terga VII–VIII with numerous posteriorly directed asperities. Female tergum VII similar to male or carina absent, with or without small rounded spine on each side of midline; tergum VIII slightly produced as a broad truncate lobe, apical margin of lobe entire, without serrations, with or without small rounded subcarinate spine on each side of midline; surface of terga VII–VIII with numerous, very large, posteriorly directed asperities, or tergum VII without asperities.

Type species. Tachiona deplanata Sharp, by monotypy.

Distribution. Presently known only from southern Mexico and Panama.

Biology. Little information is available about the biology of members of *Tachiona.* Sharp (1883) gave no data about the habitat from which specimens in the type series of *T. deplanata* were collected. Good habitat data are available for collections of *T. nitida* and *T. latipennis,* but the data are decidedly enigmatic and confusing. Adults and presumably conspecific larvae of *T. latipennis* were found together on the inside of a dense web matted with wood chips which covered a hole of about 2 inches in diameter in the trunk of a living tree. The web is about 4 inches in diameter, densely woven of coarse, irregular silken threads, which incorporate a substantial number of wood chips, and is up to 1 mm thick. The overall texture of the web is rather leathery. An adult female and larvae of *T. nitida* were also found on the inside of a very similar web over a hole in a tree. In this instance, the web was about 1.5 inches in diameter and covered a hole in a standing dead tree trunk. Except for size, the two webs were remarkably similar. We considered the possibility that the staphylinids were responsible for the webbing, but were not able to find support for this proposition. While larval aleocharines are known to produce a very fine silk for production of a pupal cocoon (Ashe, 1981; Frank and Thomas, 1984), adults are not known to produce silk. It seems unreasonable to suggest that the larvae present could have produced the coarse silk used in the webbing, or that they could have produced the very large quantity of silk present. In addition, microscopic examination of the webs revealed no sign of larval exuviae, egg cases, remnants of food, or any other sign of long term occupation by members of *Tachiona.* Since the silk webbing includes wood chips of a kind similar to those found in the holes, it seems likely that whatever produced the holes is also responsible for the covering. The best candidate for this is one of the stem-boring Lepidoptera larvae. Such bark and web capped holes have been found in association with cast skins of Lepidoptera larvae in Chiriqui by Dr.

A. Aiello (in litt.), and a head capsule of a lepidopteran larva was found in association with the web from which specimens of *T. nitida* were collected. It therefore seems unlikely that the beetles are responsible for formation of these unusual structures. However, all available biological information for specimens of *Tachiona* is remarkably consistent. Association of adults and larvae of two species, on two separate occasions, with such an unusual habitat is highly suggestive and implies that such web-covered holes may play an important role in the natural history of members of *Tachiona*.

<div align="center">KEY FOR THE SEPARATION OF KNOWN
SPECIES OF TACHIONA SHARP</div>

Only three species of *Tachiona* are known. Of these, males of *T. deplanata* and *T. nitida* have not been discovered. Therefore, separation of species based on male secondary sexual characteristics or aedeagal form, methods which are usually very effective for distinguishing among species of aleocharine staphylinids, is not presently possible. Identification of specimens of known species must be based primarily on differences in color pattern and relative proportions of antennal articles. These characteristics are very reliable for distinguishing among the specimens at hand.

1. Body color light reddish-brown, without darker markings except for small diffuse blackish patch on lateral margins of elytra; head markedly transverse, about 1.9 times as wide as long; pronotum very transverse, about 2.3 times as wide as long; antennomere II subequal in length to III; antennomeres V–X compactly arranged and very transverse, width greater than 2.4 times length .... *T. nitida*
1'. Body color reddish-flavate or light reddish-brown with distinctly darker markings on pronotum, elytra and abdominal segments; head moderately to broadly transverse, 1.5–1.8 times as wide as long; pronotum moderately transverse, not greater than 2.0 times as wide as long; antennomere II noticeably shorter than III, about 0.6–0.9 times length of III; antennomeres V–X compactly arranged or not, quadrate to moderately transverse, width not greater than 2.0 times length 2
2. Ground color reddish-flavate with markedly contrasting piceus to black markings medially and longitudinally on pronotum, and on apico-lateral 0.5 of elytra and apical abdominal segments (Sharp, 1883, pl. 6, fig. 21); antennomeres I–IV rufo-flavate and V–XI piceus to black; legs flavate with tibiae (especially near apex) darker than femora; antennomere II about 0.6–0.7 length of III, very robust and broad apically; antennomeres compactly arranged, spaces between articles less than 0.2 times length of articles .... *T. deplanata*
2'. Ground color reddish-brown, with less contrasting dark brown to piceus markings on pronotum, elytra and apical abdominal segments (Fig. 1); all antennomeres brown to piceus; legs reddish-brown, not noticeably darker near apex of tibia; antennomere II about 0.8–0.9 times length of III, not robust and only slightly broad apically; antennomeres not compactly arranged, spaces between articles greater than 0.25 times length of articles .... *T. latipennis*

<div align="center">Tachiona deplanata Sharp
Fig. 11</div>

Description. Length 5.0–6.0 mm. Body color reddish-flavate with head, median longitudinal stripe on pronotum, apico-lateral, 0.5 of elytra, posterior 0.20–0.25 of

paratergites, medial area of abdominal terga III–VII, posterior 0.5 of abdominal segment VII, and abdominal segments VIII–X darker, piceus to black. Antennal articles I–IV rufo-flavate and V–XI piceus to black. Legs flavate with tibiae darker than femora, especially near apex; tarsi piceus.

Head broadly transverse, 1.7–1.8 times as wide as long; slightly to obsoletely reticulate with irregularly isodiametric to slightly transverse sculpticells, surface shining between punctures; microsetae short, fine, appressed, moderately dense and uniformly distributed; punctures moderate in size, distance between punctures about 1.5–2.0 times as large as average width of punctures, more or less uniformly distributed. Anterior margin of clypeus deeply and broadly emarginate medially. Antenna short and robust, about as long as head and prothorax together; articles very compactly arranged, spaces between articles less than 0.2 times length of articles; article II about 0.6–0.7 times length of III, very robust and broad apically; article IV about as wide as apex of III, transverse, about 1.4 times as wide as long; article V wider than IV, transverse, 1.5 times as wide as long; articles V–X becoming slightly shorter and more transverse to article X; article X very transverse, about 2.0 times wider than long; article XI about as long as VIII–X together; antennal segments V–X distinctly flattened. Pronotum flattened and explanate dorsally, broadly transverse, about 2.0 times as wide as long, anterior margin slightly and very broadly emarginate around base of head, posterior margins broadly rounded, not bisinuate basally; microsetae fine, moderately dense, uniformly distributed; punctures moderate in size, distance between punctures about 1.0–1.5 times average width of punctures, slightly larger medially than laterally; integument between punctures smooth, shining. Elytra about 1.2 times as long as pronotum and about as wide at base as width of pronotum; sinuation of outer apical angles obsolete; punctures moderately dense, uniformly distributed, distance between punctures about 1.1–1.3 times average width of punctures, integument between punctures very obsoletely reticulate to smooth, surface shining. Tarsi robust and moderately flattened laterally. Abdominal terga and sterna with sparse setae and punctures; integument with obsolete to moderately distinct transverse microsculpture.

AEDEAGUS. Not known.

SPERMATHECA. (Fig. 11) Very complex, doubly coiled and looped.

SECONDARY SEXUAL CHARACTERISTICS. Male unknown. Female: tergum VII without medial carina, tergum VIII slightly produced posteriorly as broad truncate lobe, apical margin of lobe entire, without serrations, surface of terga VII–VIII with numerous very large, posteriorly directed asperities.

Type series. Lectotype, female, here designated, in the collection of the British Museum (Natural History), London. Lectotype has the following 5 labels: on card with specimen "Tachiona deplanata, type, D.S., Cordova, Mexico, Hoge"; a round red "type" label; "Cordova, Mexico, Hoge"; "B.C.A. Col.I.2, Tachiona deplanata Sharp"; "Lectotype, Tachiona deplanata Sharp, desig. J. S. Ashe, 1986."

Paralectotypes: 2, females, same data as lectotype (1 Field Museum of Natural History, 1 British Museum (Natural History)).

Distribution. Known only from the type locality given as "Cordova, Mexico" by Sharp (1883). Selander and Vaurie (1962, p. 68) showed this locality to be equal to Cordoba, in the state of Veracruz ("2,624 ft elev., 18°35′N 96°50′W").

Comments. See comments under *T. nitida.*

Tachiona nitida Ashe, new species

Description. Length 6.0 mm. Body color light reddish-brown throughout except for black head and small diffuse blackish patch in latero-posterior 0.5 of each elytron. Antennal articles dark brown to piceus. Legs light reddish-brown with tibiae dark brown and noticeably darker than femorae; tarsi piceus.

Head very broadly transverse, about 1.9 times as wide as long; without microsculpture, integument smooth and markedly shining between punctures; microsetae short, fine, more or less suberect, sparse and uniformly distributed; punctures moderately large, distance between punctures about 1.2–1.7 times as large as average width of punctures, more or less uniformly distributed. Anterior margin of clypeus deeply and broadly emarginate medially. Antenna short and robust, about as long as head and pronotum together; articles compactly arranged, spaces between articles about 0.2 times width of articles or less. Article II subequal in length to article III, very robust and moderately broad apically; article IV about as wide as article III at apex, broadly transverse, about 2.5 times as wide as long; article V wider than IV, broadly transverse, about 2.7 times as wide as long; articles VI–X similar in size and shape, broadly transverse, about 2.5 times as wide as long; article XI almost as long as VIII–X together; antennal articles V–X markedly flattened. Pronotum very flattened and explanate dorsally, very broadly transverse, about 2.3 times as wide as long; anterior margin broadly emarginate around base of head; posterior angles distinct, not broadly rounded; posterior margin broadly and shallowly bisinuate laterally, otherwise almost straight, not broadly rounded; microsetae fine, sparse, more or less distantly and uniformly distributed; punctures moderately large, distance between punctures about 1.5–2.0 times average width of punctures, punctures slightly larger medially than laterally; integument between punctures smooth, without microsculpture, except for very obsolete and faint transverse microsculpture in some regions, surface markedly shining. Elytra about 1.3 times as long as pronotum, outer apical angles slightly sinuate; punctures moderately dense, uniformly distributed, distance between punctures about 1.0–1.2 times average width of punctures; integument between punctures very obsoletely reticulate to smooth, surface markedly shining. Tarsi robust and markedly compressed laterally. Abdominal terga and sterna with sparse setae and punctures; integument with obsolete to markedly distinct transverse microsculpture.

AEDEAGUS. Not known.

SPERMATHECA. Very similar to that of *T. deplanata* (Fig. 11).

SECONDARY SEXUAL CHARACTERISTICS. Male not known. Female: tergum VII with very small but distinct spine on each side of midline, without medial carina or other large asperities; tergum VIII slightly produced as broad truncate lobe, apical margin of lobe entire, without serrations; surface of tergum VIII with numerous large, posteriorly directed asperities in addition to small subcarinate rounded spine on each side of midline in posterior 0.25.

Type. Holotype, a female, with labels as follows: "MEX: Veracruz, 9 Km w. Maltrata, hwy 150D, 13VIII87, J. K. Liebherr and D. A. Millman; ex. in treehole of dead stump covered with silk-like web; Holotype, *Tachiona nitida* Ashe, Desig. J. S. Ashe, 1986." The type specimen is missing antennal articles VI–XI on the right side and all tarsi on the right anterior leg. Deposited in the entomological collections of Cornell University, Ithaca, New York.

Paratypes. None. Known only from the type specimen.

Distribution. Known only from the type locality in the state of Veracruz in Mexico, near Maltrata, at an elevation of 1,900 meters.

Comments. T. nitida is known only from a single female. Normally we would consider it unwise to describe new aleocharine species without first knowing the male characteristics. However, in this instance, the known female representative of this new species is easily distinguished from all other known species of *Tachiona* by a variety of distinctive external characteristics. These features provide a sound basis for describing this species.

Among known species, specimens of *T. nitida* are most similar to those of *T. deplanata* from which they can be easily distinguished by those characteristics listed in the key as well as the larger, more sparsely distributed punctures of the head and pronotum and the distinctive female secondary sexual characteristics of *T. nitida.*

In many characteristics, *T. nitida* is the most highly derived species among known *Tachiona.* These relatively highly derived features include the very broad, transverse head and pronotum, the smooth and shining integuments, the compactly arranged, markedly flattened and very transverse antennal articles, and the very robust and laterally flattened tarsi. These features are also characteristic of specimens of *T. deplanata* and suggest a close relationship between these two species; however, they are not as markedly developed in this latter species.

Tachiona latipennis Ashe, new species
Figs. 1–10

Description. Length 5.0–6.5 mm. Body color light reddish-brown with head, posterior 0.5 and lateral areas of elytra, posterior 0.5 of tergum VI of some individuals, and terga VII–X dark brown to piceus brown. Antennal articles dark brown to piceus brown. Legs light reddish-brown, not noticeably darker near apex of tibia, some specimens with tarsi slightly darker.

Head moderately transverse, about 1.5–1.6 times as wide as long; moderately reticulate with isodiametric sculpticells to obsolete sculpture, surface shining between punctures; microsetae short, fine, moderately dense and uniformly distributed; punctures moderate in size, about as large as distance between the punctures, uniformly distributed. Anterior margin of clypeus very slightly emarginate medially. Antenna moderate in length, not noticeably robust, extended to basal 0.3–0.4 of elytra; articles more or less loosely arranged, spaces between articles greater than 0.25 times length of articles; article II about 0.8–0.9 times length of III, not robust and only slightly broad apically; article IV slightly wider than apex of III, quadrate to moderately transverse, up to 1.2–1.3 times as wide as long; article V broader than IV, shape various, slightly elongate, quadrate, or slightly transverse; articles V–X becoming progressively shorter and more transverse to article X, or little difference in shape of articles V–X; article X quadrate to moderately transverse, up to 1.8 times as wide as long; article XI about as long as IX–X together; articles VI–X very slightly flattened laterally. Pronotum flattened and explanate dorsally, broadly transverse, about 1.7–1.9 times as wide as long, anterior margin slightly and very broadly emarginate around base of head, posterior margin very slightly to obsoletely bisinuate basally; surface without sculpture to reticulate microsculpture obsolete, surface shining between punctures; microsetae fine, moderately dense, uniformly distributed; punctures moderate
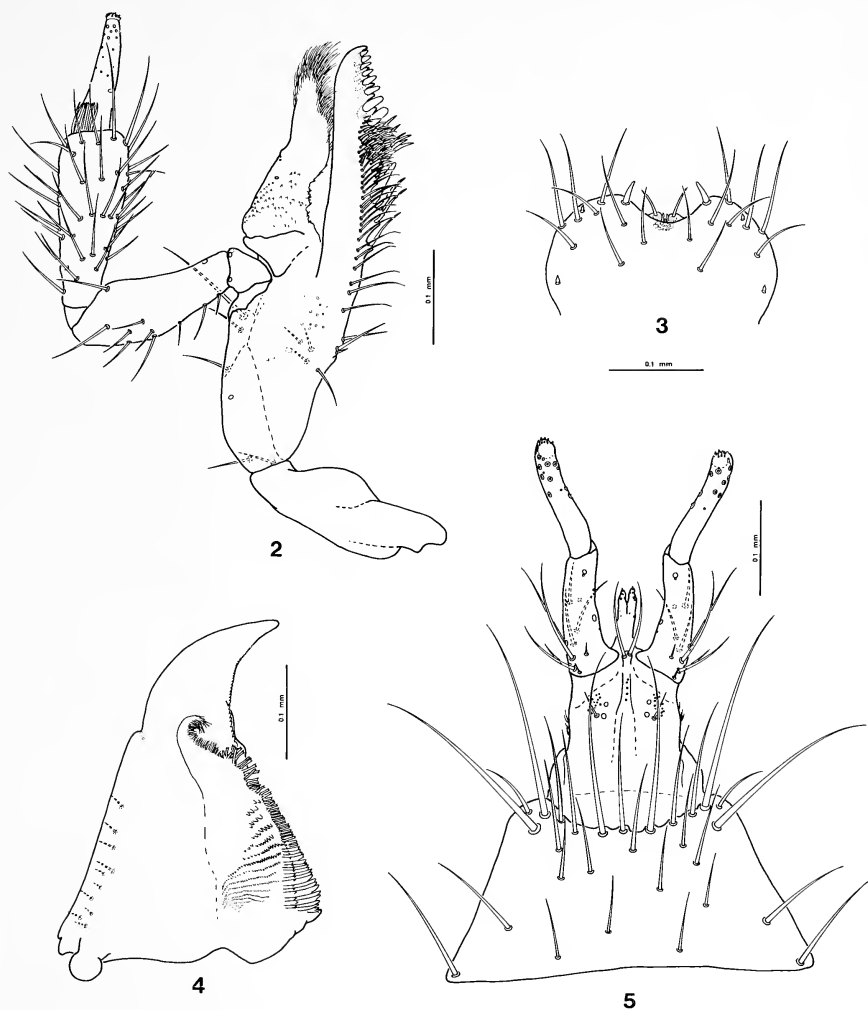
Figs. 2–5. *Tachiona latipennis* Ashe. 2. Maxilla, dorsal aspect. 3. Labrum, dorsal aspect. 4. Mandible, dorsal aspect. 5. Labium, ventral aspect.

in size and density, about as large as distance between punctures, slightly larger medially than laterally, uniformly distributed. Elytra about 1.3 times as long as pronotum and about as wide at base as width of pronotum; outer apical angles slightly and broadly sinuate; punctures moderately dense, uniformly distributed, about as large as distance between punctures; integument between punctures obsoletely reticulate, surface shining. Tarsi slightly robust and very slightly flattened laterally. Abdominal terga and sterna with moderate to sparse setae and punctures; integument with obsolete to moderately distinct transverse microsculpture.

AEDEAGUS. Median lobe (Figs. 6, 8) relatively simple with short robust apical
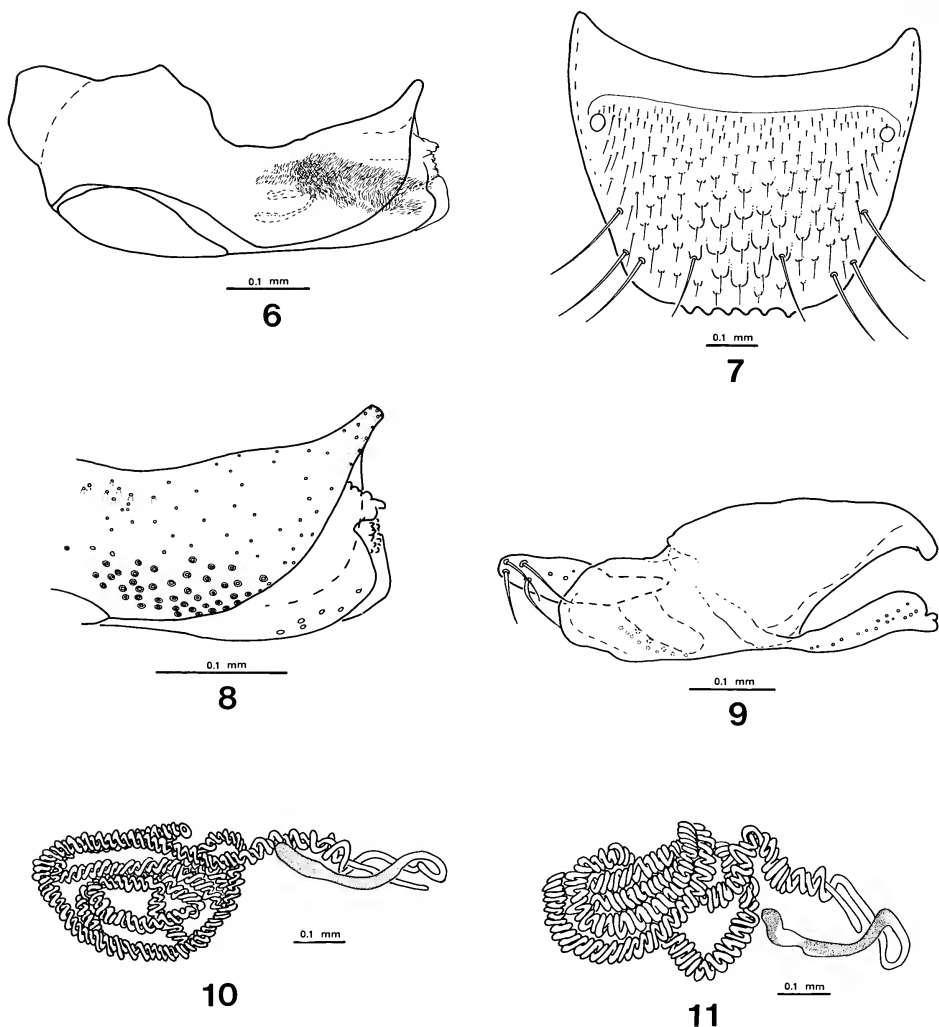
Figs. 6–11. 6–10. *Tachiona latipennis* Ashe. 6. Aedeagus, median lobe. 7. Male abdominal tergum VIII. 8. Aedeagus, apex of median lobe showing distribution and type of sensory pores. 9. Aedeagus, paramere, internal aspect. 10. Spermatheca. 11. *Tachiona deplanata* Sharp, spermatheca.

lobe and patches of fine setae internally; parameres as in Figure 9, apical lobe of paramerite with 4 setae directed toward median lobe.

SPERMATHECA. (Fig. 10) Elongate, convoluted and doubly coiled.

SECONDARY SEXUAL CHARACTERISTICS. Male: abdominal tergum VII with broad low median carina; tergum VIII produced as broad truncate lobe, apical margin of lobe with 3–4 small teeth on each half of midline; surface of terga VII–VIII with numerous, very large, posteriorly directed asperities (Fig. 7). Female: ter-

gum VII similar to male or carina absent; tergum VIII slightly produced as broad truncate lobe, apical margin of lobe entire, without serrations; surface of terga VII–VIII with numerous large, posteriorly directed asperities.

Type. Holotype, male, and allotype, female, each with labels as follows: "Panama, Chiriqui prov., nr. Nueva Swissa, 5-VIII-1978, wood chip web over tree hole, Q. D. Wheeler, lot no. 7841; Holotype (on female, Allotype), *Tachiona latipennis* Ashe, Desig. J. S. Ashe, 1986." Both holotype and allotype are deposited in the Field Museum of Natural History, Chicago, Illinois.

Paratypes. 5 (2 on microslides). All deposited in the Field Museum of Natural History, Chicago, Illinois. Same data as type.

Distribution. Known only from Chiriqui Province in Panama, near Nueva Swissa, 8°50′N 83°20′W, elevation 5,000–6,000 ft.

Comments. Specimens of *T. latipennis* retain relatively primitive states of many characters which are highly derived in other known species of *Tachiona.* The less transverse head and pronotum, somewhat more distinct microsculpture, more loosely arranged, only very slightly flattened, and quadrate to only moderately transverse antennal articles, and only slightly robust and very slightly flattened tarsi, clearly indicate that *T. latipennis* is derived more basally within *Tachiona* than is either *T. deplanata* or *T. nitida.*

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DESCRIPTION OF LATE INSTAR LARVAE OF

TACHIONA LATIPENNIS ASHE

Figs. 12–28

(Chaetotaxic system according to Ashe and Watrous, 1984)

</div>

Diagnosis. Larvae of *Tachiona latipennis* can be distinguished from all other described aleocharine larvae by the combination of: body form markedly dorsoventrally flattened and elongate oval in dorsal outline; body setae simple, of two distinctly different types, some of medium length and slightly robust mixed with darker, much longer and more or less sinuate setae (especially P2, P4 and L4 on thoracic terga, and P2 and P4 on abdominal terga III–VII) (Figs. 22, 23, 24); relatively elongate antenna (Fig. 16) with robust and slightly asymmetrical sensory appendage and solenidia IIS2 and IIIS4 fenestrate (surface appearing granulate at high magnifications, Fig. 17); distinctive pattern of spines and sensory pores on epipharynx (Fig. 19); rather long, broadly conical ligula (Fig. 21); no, or at most, very slight modification of abdominal tergum VIII in association with tergal gland (Fig. 25); tergal gland reservoir more or less membranous without sclerotized loop-like thickenings (Fig. 26); sclerotized portions of gland ducts present as 4 papillate structures (Fig. 26); and, presence of 4 large anal hooks (Fig. 27).

Description. GENERAL. Length of late instar larvae 5.0–6.1 mm (prob. not fully mature). General body form very markedly dorsoventrally flattened, broad and flat dorsally, elongate oval in dorsal outline, body widest at abdominal terga II and III. Color light yellowish-brown with lighter lines along ecdysial sutures of head and thoracic nota. Microsculpture absent except for scattered micropoints on frons and clypeus, and very fine micropoints on medio-basal half of abdominal terga V–VIII. Vestiture of medium or very long simple setae; very long setae extended laterally or suberect to erect and minutely but distinctly sinuate in middle third; most setae relatively robust and some irregularly curved (Fig. 12).
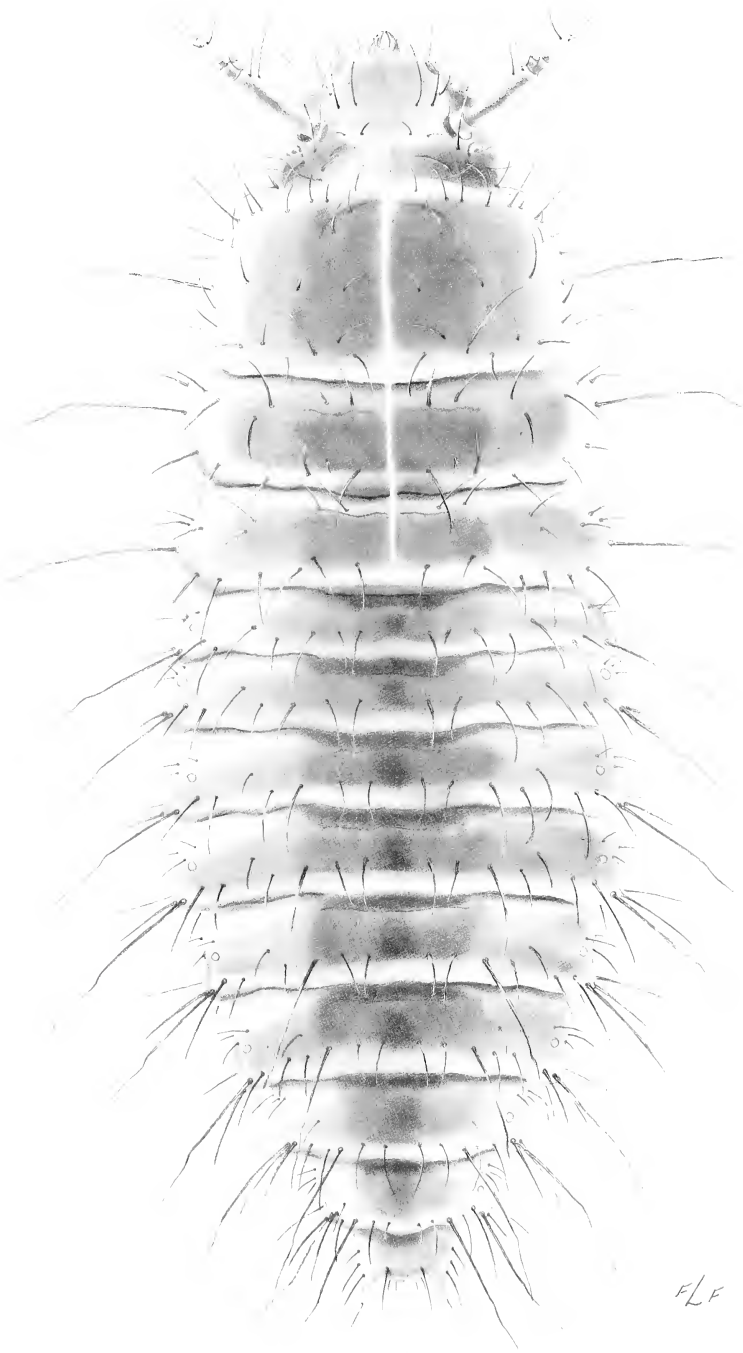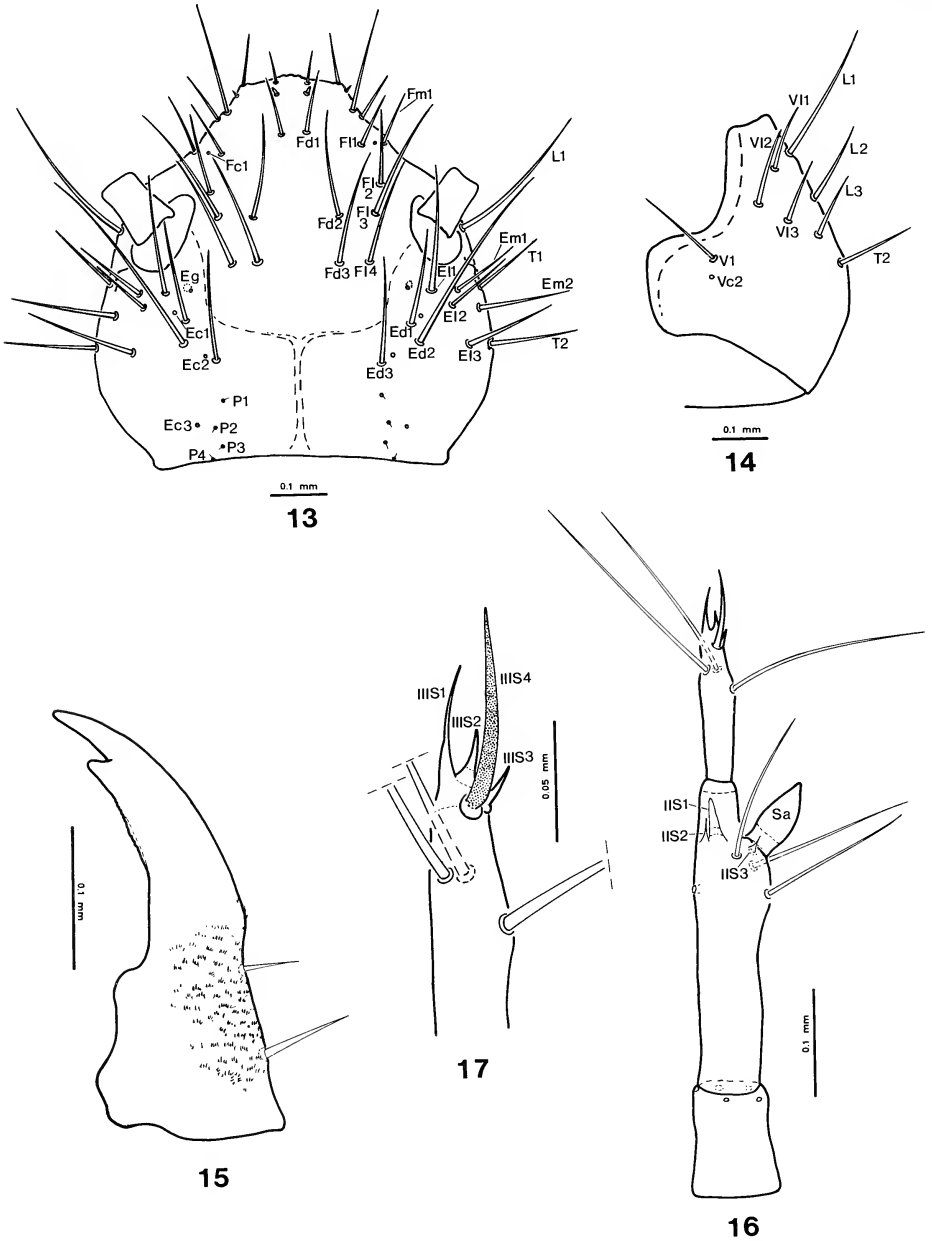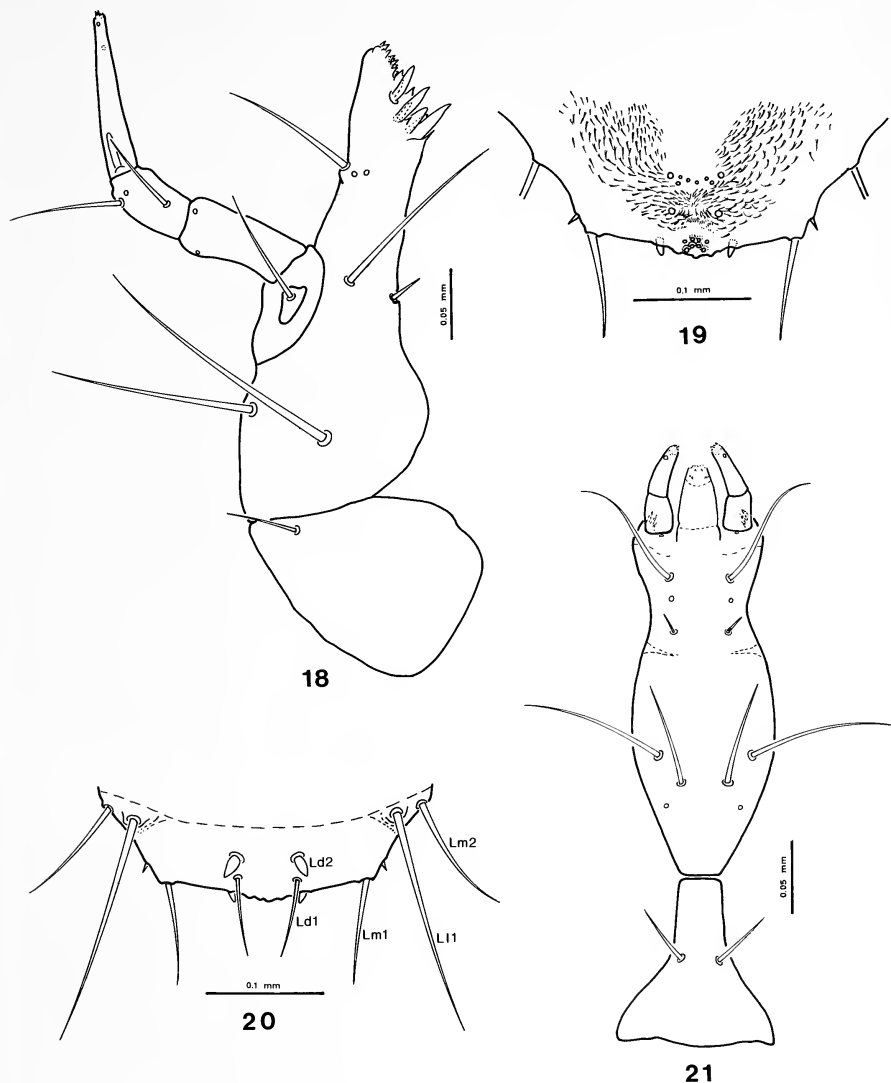
Fig. 12.   *Tachiona latipennis* Ashe, late instar larva, habitus.

HEAD. (Fig. 13, 14) About 0.9 times as wide as long. One ocellus on each side, very small. Ecdysial sutures distinct, well developed, lateral arms lyre-shaped, complete from antennal fossae to base of head. Setation as in Figures 13, 14; characteristic head setae and sensory structures present except epicranial marginal seta Em3 absent, and campaniform sensilla frontal Fc2, lateral Lc1, 2, 3 and ventral Vc1 absent; epicranial dorsal seta Ed2 noticeably longer than other epicranial setae (0.35–0.5 times longer), and lateral seta L1 about 0.5 times longer than L2-3. Antenna as in Figures 16, 17, 3-articled; article I elongate, about 1.3 times as long as wide, with 5 campaniform sensilla around apical margin; article II about 2.8–2.9 times length of article I, constricted apical portion about 0.13–0.15 times total length of article; article III about 0.5 times length of II, article II with 3 solenidia (Fig. 16, IIS1–3) in addition to sensory appendage; sensory appendage robust, inflated, slightly asymmetrical in lateral aspect and slightly constricted apically into an indistinct nipple, about 1.2–1.3 times length of constricted portion of antennomere II; solenidium IIS1 digitiform, slightly rounded at apex, about 0.6 times length of sensory appendage, distinctly and densely fenestrate (appearing granulate) when viewed at magnifications greater than 200×; IIS2 spinose and filiform, about 0.5–0.7 times length of IIS1; antennomere III with 4 solenidia (Fig. 17, IIIS1–4); IIIS1 about 2.0 times length of IIIS2, slightly inflated in basal 0.3 and filiform in apical 0.7; IIIS2 somewhat robust and thick, slightly spiniform; IIIS3 spiniform and setose, about as long as IIIS2; IIIS4 large, in a distinct socket, 1.8–1.9 times as long as IIIS1, distinctly and densely fenestrate (appearing granulate) when viewed at magnifications of 200× or greater. Labrum as in Figure 20, indistinctly or not separated from clypeus by a suture; without broadly oval internal band of sclerotization; setation consisting of 5 setae on each side, Ll1 and Lm2 located on a small lateral sclerite which is indistinctly separated from the main body of the labrum by a suture; seta Ld2 very short, robust and inflated, seta Ld1 long and filiform. Epipharynx (adoral surface of labium) as in Figure 19. Mandibles (Fig. 15) with right and left nearly identical in size and shape, slender, with pronounced preapical tooth internally and pronounced and distinct lobe in molar region; two setae in baso-lateral half large and well developed, more basal seta larger than distal seta; basal half of ventral and lateral sides with numerous very fine micropoints in short irregular rows. Maxilla as in Figure 18; cardo broadly oval, indistinctly divided internally by a sclerotized ridge, with one seta on ventro-lateral surface; stipes broad at base, not distinctly separated from mala, surface with 2 large setae, 1 on disc and 1 near lateral margin; mala with apex acutely oblique, adoral margin with spinose setae and numerous blade-like scales, most proximal scale longer than wide, dorsal surface with numerous minute cuticular micropoints in short irregular rows. Maxillary palpus (Fig. 18) of three articles in addition to basal crescentic palpifer; article I elongate, about 2.0 times as long as wide; article II about 0.75 times as long as I; article III about 0.8–0.85 times as long as I and II together; article III with basal digitiform sensory appendage on external surface. Adoral surface of labium (hypopharynx) with numerous short rows of antero-medially directed short spines. Labium (Fig. 21) consisting of fused prementum and mentum and distinctly separated (by a distinct suture) submentum; ligula elongate, broadly cone-shaped and rounded apically, about 2.0 times as long as greatest width, slightly sclerotized in apical 0.3, about 0.8–0.85 times as long as labial palps; labial palps of two articles, article II about 1.4–1.5 times as long as I; submentum with 1 pair of setae; mentum with 2
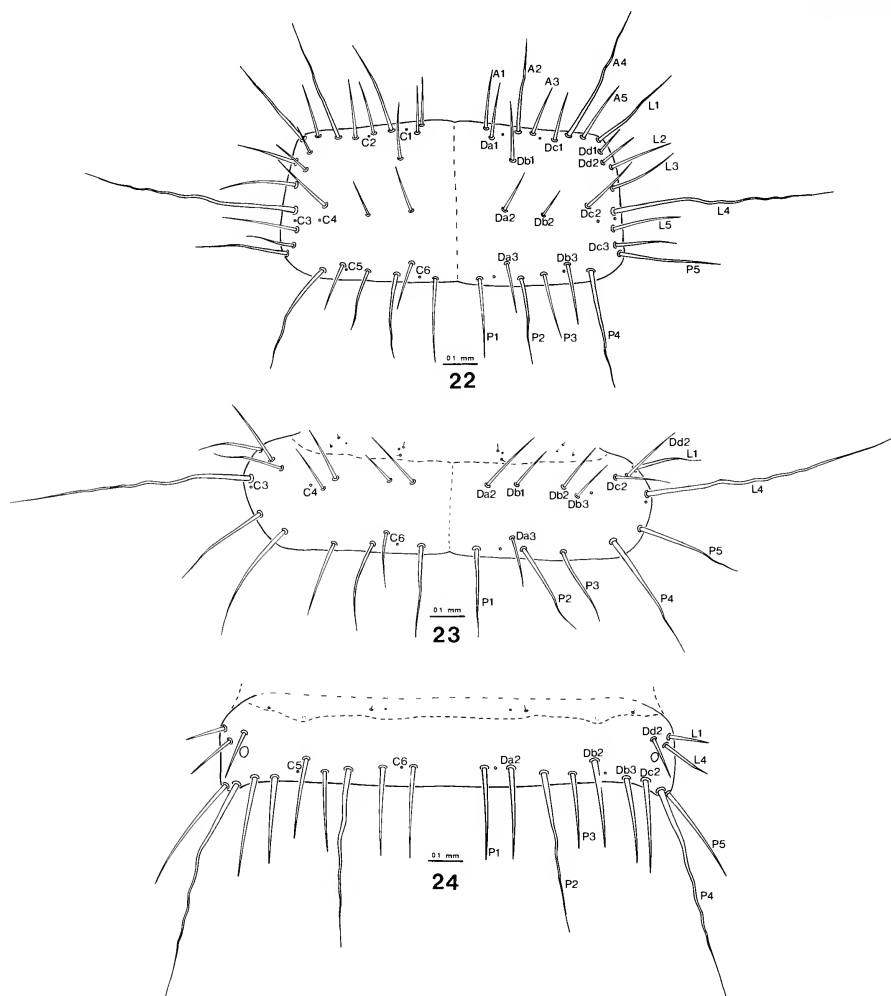
Figs. 13–17.   *Tachiona latipennis* Ashe, late instar larva. 13. Head, dorsal aspect. 14. Head, ventral aspect. 15. Mandible, dorsal aspect. 16. Antenna, ventral aspect. 17. Antenna, apical segment, ventral aspect (symbols according to Ashe and Watrous, 1984).

Figs. 18–21. *Tachiona latipennis* Ashe, late instar larva. 18. Maxilla, ventral aspect. 19. Internal surface of labrum, epipharynx. 20. Labrum, dorsal aspect. 21. Labium, ventral aspect (symbols according to Ashe and Watrous, 1984).

pair of setae and 1 pair of campaniform sensilla; prementum with 2 pair of setae and 2 pair of campaniform sensilla.

THORAX. Pronotum (Fig. 22) transverse; chaetotaxy with anterior, lateral and posterior rows complete (each with 5 setae) and discal rows complete (Da–c each with 3 setae and Dd with 2 setae), without accessory setae, lateral seta L4 very long

Figs. 22–24. *Tachiona latipennis* Ashe, late instar larva. 22. Pronotum. 23. Mesonotum. 24. Abdominal tergum IV (symbols according to Ashe and Watrous, 1984).

and sinuate in apical 0.5, anterior setae A2, A4 and posterior setae P2, P4 also longer than other setae and more or less sinuate in apical 0.5; campaniform sensilla C1–6 present. Mesonotum as in Figure 23; discal setae Da1, Dc1, Dc3 and Dd1 absent; seta Db1 located medial to Db2; lateral setae L2, L3 and L5 absent, L4 very long and sinuate in apical 0.5; campaniform sensillum C5 absent. Metanotum similar to mesonotum.

ABDOMEN. Abdominal terga I–VII very transverse; chaetotaxy as in Figure 24; discal setae Da1, Db1, Dc1, Dd1, Da3 and Dc3 absent; discal setae Da2, Db2 and Dc2 in or very near posterior row; lateral setae L2, L3 and L5 absent, L4 short, not sinuate apically; posterior seta P4 very long and sinuate in apical 0.6; posterior seta
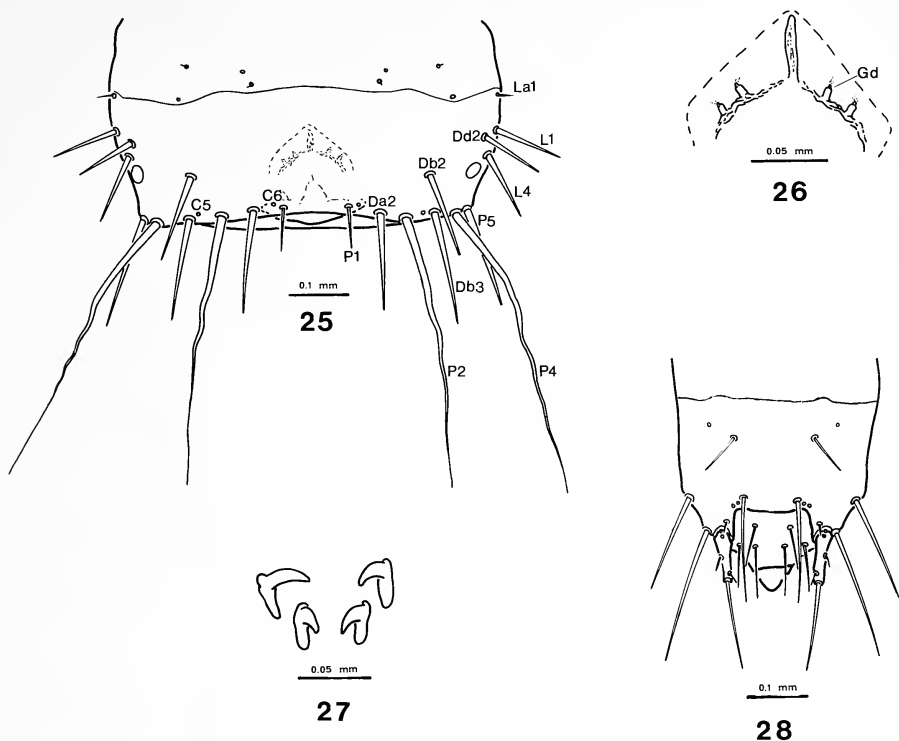
Figs. 25–28. *Tachiona latipennis* Ashe, late instar larva. 25. Abdominal tergum VIII. 26. Tergal gland and associated structures of segment VIII. 27. Anal hooks, drawn *in situ* as withdrawn into abdominal tergum X. 28. Abdominal terga IX–X (symbols according to Ashe and Watrous, 1984).

P2 longer on more posterior terga than on more anterior terga, only slightly longer than, and very similar to, P1 on tergum I, increasing in length in each successive tergum such that P2 at least 2.0 times longer than P1 and sinuate in apical 0.5 on tergum IV; tergal setae, other than very long setae, rather thick and robust. Abdominal tergum VIII (Fig. 25) not noticeably produced dorsally or postero-medially in association with tergal gland; chaetotaxy similar to that of terga I–VII except for an additional seta in the lateral row (La1), discal setae Da2 and Db3 are in the posterior row, posterior seta P1 is very small and slender, less than 0.35 times length of Da2, posterior setae P2 and P4 are very long and sinuate in apical 0.7, P3 and Pa1 absent. Tergal gland reservoir (Fig. 26) not noticeably developed externally; sclerotized portions of gland ducts cylindrical, terminating in small nipple-like structures distal to the reservoir sac; gland reservoir slightly sclerotized, less than 0.5 times length of tergum VIII. Abdominal terga IX–X as in Figure 28; urogomphus single articled, short, about 0.3 times length of tergum IX, each urogomphus displaced from main body of tergum IX on a short posterior elongation of postero-lateral margins of the tergum. Pseudopodal hooks present (Fig. 27), 2 pair, very large and well developed, withdrawn into tergum X in repose.

Fig. 29.   *Diestota rufipennis* Casey, spermatheca. Scale bar = 0.1 mm.

Material examined. 16, all instars except instar I (7 on microslides). Same data as adults.

Comments. Ashe and Watrous (1984) chose an athetine larva as a base for their nomenclatorial system for setae because of the relatively complete set of setae found on these larvae. It is interesting that except for absence of some campaniform sensilla of the head, the chaetotaxy of larvae of *T. latipennis* differs very little from that described by Ashe and Watrous (1984) for larvae of *Atheta coriaria* Kr. However, the development of individual setae is very different and provides a number of diagnostic characteristics.

Other features show more striking difference from those of athetine larvae. These include: the rather elongate, broadly conical ligula (very slender and slightly narrowed medially among athetine larvae); the structure of the teeth on the mala of the maxilla, particularly the small slender basal spine (usually broader than long among athetine larvae); and, the structure and distribution of sensory elements and other structures on the epipharynx (compare with Ashe and Watrous 1984, fig. 11). These structures are more similar to features of larvae of *Bolitochara* and *Leptusa* than to athetines.

One of the most striking sets of differences among larvae of *Tachiona latipennis* and known larvae of other members of the tribe Bolitocharini involves characteristic features of tergum VIII and associated glandular structures. Larvae of the bolito-charine subtribes Bolitocharina (based on examination of larvae of several species of *Bolitochara* and *Leptusa,* unpublished data) and Gyrophaenina (Ashe 1986) have

a prominent posterior prolongation and enlargement of tergum VIII associated with a very large gland reservoir. In addition to large size, the reservoir is also moderately to markedly sclerotized and is strengthened by distinctive sclerotized loop-like thickenings (see Ashe 1986, fig. 59). Also, the four gland ducts are represented by sclerotized tubes.

In contrast, tergum VIII of larvae of *T. latipennis* is not noticeably enlarged in relation to the gland reservoir, and there is very little external indication of the tergal gland. In addition, the gland reservoir is virtually unsclerotized and is without loop-like thickenings, and the sclerotized portions of the gland ducts are short papillate structures rather than tube-like.

This degree of difference in these characteristics is especially surprising because of the apparent close relationship between members of the subtribes Silusina and Bolitocharina as suggested by adult structure. Since confidently identified larvae of other genera of the Silusina are not known, it is impossible to evaluate whether the tergal gland structure exhibited by larvae of *T. latipennis* is characteristic of the subtribe.

Since larvae are associated rather than reared, the possibility that they are misidentified must be considered. The reasons that the larvae described here are believed to be conspecific with adults of *Tachiona latipennis* include: the larvae were found in relatively large numbers in association with numerous adults of that species; only a single species each of larvae and adults were included in the collection; the flattened and broad body of the larvae correctly reflects the explanate body of adult *Tachiona*; the largest larvae are in a size range which would be expected of larvae of this species; and, structure of the ligula, epipharynx and maxilla (but not the tergal gland structures) is typical of other bolitocharines and different from those of athetines, oxypodines or known members of other tribes. Taken in concert these represent compelling evidence that the larvae described here are correctly associated. In addition, discovery of very similar larvae in association with adults of *Tachiona nitida* adds considerable strength to this proposition.

Comparison with larvae of Tachiona nitida *Ashe.* Larvae of *T. nitida* are very similar in general habitus, color, chaetotaxy, and detailed structure to those of *T. latipennis*. Late instar larvae of *T. nitida* differ in the following features: dorsum of head with epicranial campaniform Ec2 absent, epicranial dorsal seta Ed2 very large and slightly sinuate; venter of head with ventral campaniform sensilla Vc2 absent and Vc1 present; antennal solenidium IIS2 somewhat more distant from IIS1, IIS3 slightly smaller, and sensory appendage of antennomere II not as asymmetrical; chaetotaxy of abdominal terga with posterior seta P2 not noticeably longer than P1 on terga I–IV, but P2 very large, dark and markedly sinuate on terga V–VIII.

Eight larvae, of all instars, of *Tachiona nitida* were available for examination. One of these was much larger and fatter than the others, with sclerites widely separated by extensive areas of intersegmental membrane. It seems possible that this individual may be a prepupa.

Early instar larvae. First instar larvae of *T. latipennis* were not available; however, first instar larvae of *T. nitida* are similar in habitus and general structure to later instar larvae, except that the chaetotaxic pattern is similar to that described for first instar *Atheta coriaria* Kr. (Ashe and Watrous 1984:178) though size and structure of many setae differ markedly from comparable setae of *A. coriaria*. In addition to this difference in chaetotaxic pattern, first instar larvae of *T. nitida* differ from those of

later instar larvae in the following ways: antennal articles much shorter, antenna short and stout; antennal solenidium IIS3 absent; antennomere III with dark pigment throughout; molar lobe of each mandible extended adorally into a minute but distinct spine; dorsal surface of head with prominent hatching spine on each side of midline medial to epicranial posterior seta P1; pronotal lateral seta L4 large but not noticeably darker or more sinuate than other pronotal setae, posterior setae P2 and P4 larger than other posterior setae but not sinuate; mesonotal lateral seta L4 very large, dark and markedly sinuate, posterior setae P2 and P4 similar to those on pronotum; metanotum similar to mesonotum, hatching spines absent; abdominal terga I–VIII with posterior setae P2 and P4 variously developed; posterior setae P2 and P4 on abdominal terga I–IV similar in size and structure, larger than other posterior setae, and not sinuate; posterior seta P4 on abdominal terga V–VIII much larger and darker than on more anterior terga and markedly sinuate; posterior seta P2 on abdominal terga V–VII larger than all posterior setae except P4 but not noticeably darker or sinuate; posterior seta P2 on abdominal terga VIII very large, dark and markedly sinuate; gland reservoir of abdominal tergum VIII somewhat fainter; gland ducts very slightly sclerotized, tube-like, very thin and irregularly looped; urogomphi typical of first instar aleocharine larvae, about as long as tergum X, thin, slightly recurved near base, each with a very long apical seta and a much shorter preapical seta; anal hooks 4, very large and prominent.

The most unusual feature of these first instar larvae, other than those unusual features that characterize *Tachiona* larvae in general, is the presence of hatching spines on the dorsum of the head and the absence of such spines elsewhere on the body. Most first instar aleocharine larvae have hatching spines medio-posteriorly on the metathorax and, in specimens of some species, on one or more anterior abdominal terga (Ashe and Watrous, 1984; Ashe, 1986). We are not aware of any other aleocharine larvae, either described or undescribed, which have hatching spines on the head.

DISCUSSION

Sharp (1883) made special mention of the unusual body form of members of *Tachiona* and noted that they showed considerable resemblance to members of the genera *Dinusa* Saulcy and *Dinarda* Mannerh., both of which are in the tribe Oxypodini. However, *Tachiona* did not appear to him to be related to these genera. Instead, he was correct in noting that *Tachiona* must be placed in the "group Bolitocharaires of Rey" (p. 284) (probably referring to Mulsant and Rey, 1871). In addition to tarsal formula, Sharp also noted that the members of *Tachiona* had maxillary lobes that were elongate and prominent, but he incorrectly observed the labial palpi to be short and inconspicuous. However, Mulsant and Rey's grouping was based primarily on the shared presence of a 4,4,5 tarsal segmentation, and, as a result it contained a structurally diverse grouping of genera.

By the time *Tachiona* was next mentioned in the literature by Fenyes (1918, 1920) it was apparent that subdivisions of the heterogeneous assemblage of genera in the tribe Bolitocharini (approximately equal to the Bolitocharaires of Rey) were necessary. Fenyes (1918) recognized 14 "groups" within the tribe Bolitocharini and placed *Tachiona* in the "Group Leptusae" based apparently on the incorrect description of the mouthparts provided by Sharp.

The only other mention of *Tachiona* was by Bernhauer and Scheerpeltz (1926). They likewise classified the genus based on Sharp's description and Fenyes' placement. They combined Fenyes' groups Leptusae and Bolitocharae into the subtribe Bolitocharae, within which they included *Tachiona.*

Since neither Fenyes nor Bernhauer and Scheerpeltz appear to have examined specimens of *Tachiona,* they could not have known that this genus is more correctly placed in the subtribe Silusina (group Silusae of Fenyes, subtribe Silusae of Bernhauer and Scheerpeltz).

Among aleocharines that have 4,4,5 tarsal segmentation, the subtribe Silusina is characterized by the distinctive styliform labial palpi and the elongate and prominent maxillary lobes (Lohse, 1974; Seevers, 1978). Based on our examination of the structural features of nine silusine genera (*Diestota* Muls. and Rey, *Elachistartheron* Notm., *Neosilusa* Cam., *Ousilusa* Cam., *Plagiusa* Bernh., *Pseudoplacusa* Cam., *Stenomastax* Cam., *Silusa* Er., and *Tachiona* Sharp), the members of this subtribe have a striking number of similarities, especially in mouthpart structure. Most characteristic is the detailed structure of the styliform labial palpi. The suture between the basal and the second labial article is fused and virtually indistinguishable. This gives the appearance of long, slender two-segmented labial palpi. In addition, the apical segment is divergent and recurved such that the field of sensory structures at the apex is directed slightly to moderately inwardly rather than anteriorly as it is among most other aleocharines. Distinctive features are also found on the prementum. The two medial setae of the prementum are placed very close together, and the medial pseudopore field is narrowed laterally so that medial pseudopores (see Sawada, 1972) are compressed into a narrow longitudinal row. They also have two "real pores" medial to the "setose pore" in each lateral field (terms for porose structures according to Sawada, 1972). While other aleocharines may have some of these labial characteristics, this combination appears to be unique to silusines.

The maxilla of silusines is also very distinctive, especially among those aleocharines with 4,4,5 tarsal segmentation. Both galea and lacinia are elongate. Most striking is the relatively long narrow apical third of the lacinia, with its single row of more or less widely dispersed teeth (especially long and narrow among members of *Silusa*). The dense patch of spinose setae near the middle and the well defined longitudinal row of setae dorsally on the lacinia are also distinctive.

All of these characteristics are well illustrated in the mouthparts of *Tachiona* (Figs. 2, 5).

Members of other groups of aleocharines are also characterized by stylate labial palpi and elongate maxillary lobes. This is especially evident among members of *Myllaena* and related groups, though such modified mouthparts are not limited to this group. However, the details of mouthpart structure are very different between these groups and members of the Silusina.

Lack of a strong comparative base makes it very difficult to evaluate primitive and derived states of many mouthpart characters found among aleocharines. Nonetheless, the limited distribution of many states found among silusines (in comparison to several other distinct lineages) suggests that at least some are likely to be uniquely derived apomorphies. This provides considerable evidence that members of the subtribe Silusina form a monophyletic group. Yet the secondary sexual characteristics of some silusines (especially *Silusa*) and their general habitus show a remarkable

similarity to those of *Bolitochara* (in a broad generic sense) (subtribe Bolitocharina). The crenulate hind margin of male tergum VIII as well as the presence of a medial knob or carina on tergum VII and the triangular posterior projection of sternum VIII among males of *Bolitochara* and *Silusa* makes it difficult to avoid the conclusion that they are closely related. This contrasts markedly with the very different mouthparts of members of these two genera.

Among silusine genera, the, broad, flattened body form of members of *Tachiona* is highly distinctive. However, they share an unusually large suite of characteristics with members of *Diestota* Mulsant and Rey. These include: 1) mesocoxal cavities very widely separated by broad meso- and metasternal processes; 2) bifid ligula and similar distribution of pores on the prementum of the labium; 3) similar distribution of denticles in the molar region of the mandibles-denticles arranged in distinct transverse rows with the largest denticles in the most distal row (Fig. 4); and, 4) remarkable similarities in the spermatheca and aedeagus. Among these similarities, those in the spermatheca and aedeagus seem most significant.

The spermatheca of females of *Diestota* are very unusual. The neck of the spermatheca is greatly elongated and is tightly doubly coiled with a smaller coil inside the tube formed by the outside coil (Fig. 29) (based on examination of *D. brasiliana* Bernh., *D. laticornis* Sharp, *D. luederwaldti* Bernh., *D. obsoleta* Er., *D. rufipennis* Csy., and *D. testacea* Kr.). The distinctive features are very similar among all species of *Diestota* examined (see also illustration of spermatheca of *D. luzonica* Bernh., Sawada, 1971, fig. 2I). These are very similar to the complex doubly coiled and convoluted spermathecae of members of *Tachiona* (Figs. 10, 11). The spermathecae of *Tachiona* and *Diestota* are also similar in that the basal bulb is elongate and is divided into distinctive anterior and posterior sections by a very slightly sclerotized medial region (note basal bulb in Figs. 11, 12, and 29). Size and shape of these sclerotized portions of the basal bulb of the spermatheca is remarkably similar among examined members of these two genera. Members of other silusine genera examined have simple spermathecae.

Equally striking are similarities in the aedeagus. The median lobes of examined members of *Diestota* (*D. angustula* Csy., *D. brasiliana* Bernh., *D. laticornis* Shp., *D. luederwaldti* Bernh., *D. obsoleta* Er., *D. rufipennis* Cys., and *D. testacea* Kr.) and *Tachiona latipennis* are similar in that the apical process is broad, tent-like, and simple, and is covered with a distinctive pattern of numerous pore-like sensory structures. The apical process of all species examined in both genera has two distinct types of pore-like structures. The more basal ones are very large and appear to be doubly ringed because the edges are apparently raised into a fine ridge. The more dorsal pores are simpler and appear as unmodified holes in the cuticle under light microscopy (Fig. 8). I have not seen a similar pattern of sensory structures among median lobes of other silusines that I have examined, though both types of sensory structures may be present in other patterns on the median lobe of other species.

Clearly, until considerably more comparative study of a wider variety of genera and species in the Silusina and related subtribes has been completed generic relationships within the subtribe must remain obscure. Thus it is premature to strongly advocate a close relationship between *Tachiona* and *Diestota* within the Silusina. However, the similarities discussed above are highly suggestive, and should provide

the basis for more detailed examination of character states among silusine and related aleocharine genera.

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SYRPHIDAE (DIPTERA) DESCRIBED FROM UNKNOWN LOCALITIES

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Abstract.—Names of 66 flower flies described by earlier authors from unknown localities are revised. Seven unused senior synonyms are resurrected [*Spilomyia alcimus* (Walker, 1849) (=*hamifera* Loew, 1864), *Criorhina bubulcus* (Walker, 1849) (=*luna* Lovett, 1919), *Temnostoma daochus* (Walker, 1849) (=*pictulum* Williston, 1887), *Eristalinus dives* (Walker, 1849) (=*vitrescens* Hull, 1937), *Volucella linearis* Walker, 1849 (=*nitobei* Matsumura, 1916), *Copestylum longirostre* (Macquart, 1846) (=*concinna* Philippi, 1865), & *Chalcosyrphus violascens* (Megerle, 1803) (=*chalybea* Wiedemann, 1830)]; 22 other new synonyms are identified [*Eristalinus aeneus* (Scolpoli, 1763) = *aenescens* Macquart, 1842, *Prohelophilus cingulata* (Fabricius, 1775) = *agerinus* Walker, 1849, *Neocnemodon vitripennis* (Meigen, 1822) = *albohirta* Wiedemann, 1830, *Eriozona syrphoides* (Fallén, 1817) = *amplus* Walker, 1849, *Eristalinus arvorum* (Fabricius, 1787) = *anicetus* Walker, 1849, *Milesia crabroniformis* (Fabricius, 1775) = *coenina* Walker, 1849, *Xylota florum* (Linnaeus, 1758) = *corbulo* Walker, 1849, *Chalcosyrphus metallicus* (Wiedemann, 1830) = *dascon* Walker, 1849, *Merodon aureus* (Fabricius, 1805) = *flavicornis* Macquart, 1842, *Copestylum brunneum* (Thunberg, 1789) = *fusca* Macquart, 1834, *Pipizella viduata* (Linnaeus, 1758) = *fuscipennis* Walker, 1849, *Eristalis dimidiata* Wiedemann, 1830 = *haesitans* Walker, 1849, *Palpada furcata* (Wiedemann, 1830) = *involvens* Walker, 1849, *Eristalinus quinquelineatus* (Fabricius, 1781) = *jucundus* (Walker, 1849), *Brachypalpus laphriformis* (Fallén, 1816) = *laphriaeformis* Walker, 1849, *Helophilus groenlandicus* (O. Fabricius, 1780) = *oxycanus* Walker, 1852, *Meromacrus acutus* (Fabricius, 1805) = *pictus* Macquart, 1846, *Phytomia zonata* (Fabricius, 1787) = *rufitarsis* Macquart, 1842, *Eristalinus taeniops* (Wiedemann, 1830) = *secretus* Walker, 1849, *Chrysotoxum intermedium* (Meigen, 1822) = *stipatum* Walker, 1852, *Palpada mexicana* (Macquart, 1847) = *tomentosus* Macquart, 1850, & *Orthoprosopa grisea* (Walker, 1835) = *torpidus* Walker, 1857]; 3 new combinations are established [*Palpada caliginosus* (Walker, 1849), *Eupeodes corolloides* (Macquart, 1850), & *Mesembrius strenuus* (Walker, 1857)]; one old synonym is reestablished [*Quichuana angustiventris* (Macquart, 1855) = *aurata* Walker, 1857]; and 15 old synonyms confirmed. *Eumerus aquilinus* Walker is redescribed and its genitalia figured. Location of types and labels of Bigot, Macquart, Megerle, Walker and Wiedemann are described.

Flower flies are important pollinators, and the maggots of many species are predators of homopterous pests, such as aphids and scales, while a few maggots feed on economically important plants. Names are essential for communicating about complex objects such as species. Confusion, however, can arise when two different names are used for the same species, and the same name for two different species! This paper clarifies the status of 66 names used for flower flies so as to aid proper communications about these beneficial pollinators and predators.

During the early part of the last century a number of species were described from unknown localities (*patria ignota*). As most systematic work is done on a regional basis, these earlier *patria ignota* names have been neglected. Despite this neglect

these names are available and pose a serious threat to the stability of nomenclature. This paper lists all the *patria ignota* names (66) known to apply to Syrphidae and attempts to identify their provenance and possible synonymy. The names are treated in alphabetic order. For each name the following is given: The name as originally spelled (including capitalization), original citation, type-locality as originally given, type-depository, and the current status of the name and distribution of the species to which the name applies.

My use of the word "identification" here is slightly different from the conventional one. A name must have been accompanied by a diagnosis, description or indication that functions to "identify" the concept that the name denotes. Hence, I used the word "identification" for the process by which a name is tied to a concept, whereas the usual connotation of "identification" is tying a concept to a name.

TYPE DEPOSITORIES AND LABELS

I have not described the labels of most of the types individually; instead the general characteristics of these labels are described, and the locations of the types of Bigot, Macquart, Megerle, Walker and Wiedemann are noted.

Bigot types are divided between the University Museum at Oxford and the British Museum (Natural History), London. Bigot was a wealthy French amateur who amassed a fine library and a great collection of flies. He purchased Diptera from the collections of others, such as Fairmaire and Serville, and had his material studied by Macquart. Hence, many Macquart types are in Bigot's collection. His collection was sold to G. H. Verrall. Verrall, who apparently intended that this collection would one day go to the British Museum, during this lifetime turned over many exotic types from the Bigot collection to the British Museum. However, the bulk of his collection was passed on to his nephew, J. E. Collin. Collin, at the end of his life, decided that these collections would be better placed at Oxford than at the British Museum. Hence, the types of Bigot and those of Macquart in the Bigot-Serville-Fairmaire collection may be found either in Oxford or London. The types in the British Museum are usually labeled with a "Verrall donation" label (Fig. 7) and there is frequently a cross-reference label in the collection at Oxford. Usually, one of the types has the Macquart name label or a Bigot/Macquart name label folded up on the pin. Bigot frequently glued the original Macquart name label on to one of his labels (Fig. 7). The collection at Oxford was well described by Ackland and Taylor (1972) (also Maa, 1963:175). In Oxford, there are basically three components: the "Exotic" collection (4 drawers of syrphids), the Palaearctic collection (4 drawers), and the British Collection (7½ drawers), with some material in the excess collection.

Macquart types are scattered among a number of museums, with his personal collection deposited in Lille. The depository of his types is usually given in the original description. For the syrphids, the following are given with their present locations: Bigot, 56 species, q.v.; Breme, 1, see under *pictus*; Fairmaire, 12, in Bigot; Latreille, 2, see under *pictus*; Lefebvre, 2, unknown; Macquart, 50, in Lille; Museum, 109, in Paris; Payen, 4, unknown; Percheron, 2, unknown; Pilate, 1, unknown; Robyns, 4, in Brussels; Serville, 21, in Bigot; Spinola, 2, in Turin; and Webb & Berthelot, 4 Canary Island species, mostly destroyed but remains are in Paris; and not indicated, 31, in various collections. Macquart types can usually be identified by the name label in his distinctive hand (Fig. 11). In all the museums where I have seen Macquart

material this label is folded up and placed on the pin of one of the types. The respective curators have then added their own labels. The Macquart material in Paris was for many years in the general collection, but Séguy removed it and placed it in a separate collection. Hence, some of the missing Macquart types may still be in the general collection. "This is especially the case with French material, originating from Macquart's own collection and not recognized as syntypes by Séguy" (Pont, in litt.). This is unlikely for syrphids, as I and others (Vockeroth, Speight et al.) have carefully examined the general collections for types.

Megerle material should all be in the museum at Vienna. He was an early dealer in insect material and published a number of sale catalogs. Wiedemann redescribed two species first named in Megerle's sale catalogs (*Pygrota undata* Megerle and *Hippobosca variegata* Megerle). The material used for these redescriptions is now in Vienna and may have arrived there via the Wiedemann/Winthem collections. Meigen described a number of species from material from "Hrn. Megerle von Mühlfeld" as well as from "Kais. Königl. Museum." Horn & Kahle (1936:171) stated that Megerle was the curator of the Imperial Museum in Vienna as well as the founder of an auction house for natural history specimens, especially insects, in Vienna from 1798–1806; that his first private collection went to the museum in Vienna in 1808; that his posthumous collection was also deposited in Vienna via J. A. Ferrari (after 1848?). Whether Meigen used the different form of depository citation to differentiate between what was Megerle's private material and what he may have borrowed from the Imperial Museum is not clear. These collections could both have been part of the Imperial Museum, but just kept separate as most collections were at that time. The important point here is that, if both citations do refer to material that was part of the Imperial Museum, then most of the material was destroyed in the fire of 1848. I assume that this is the case, as I have found very little Megerle material that was not part of the Wiedemann/Winthem collections (q.v.). If Meigen's citation of "Megerle von Mühlfeld" refers to the "posthumous" collection, then that material would have arrived at the museum after the fire and would today be labeled as "Alte Sammlung." Hence, any Megerle material extant today should be labeled "Alte Sammlung." A number of specimens that Wiedemann described as from unknown localities and from the "Wiener Museum" are probably Megerle material. Many of these specimens have a curious "F" label in addition to the "Alte Sammlung" label (*Baccha fusciventris, Baccha costalis, Hippobosca variegata,* etc.).

Walker types are usually found in the British Museum (Natural History) in London, although a few are at Oxford (Smith and Taylor, 1964). These types are clearly identified by a green circular "Walker" type label (Fig. 8) and usually a name label written by E. E. Austen (Fig. 8, 10) or E. A. Waterhouse. "Material that was in the Museum and was described in the 'List' [Walker, 1849] is labeled by E. A. Waterhouse as 'one of Walker's specimens so named' with the species name. Material that came from Saunders, including the Wallace material, usually has Walker's original label preserved" (Pont, in litt.). Sometimes, Austen merely wrote the name on the green Walker type label. Rarely, the original name label in Walker's hand has been folded up and saved on the pin (Fig. 14). Austen (1893) curated the Syrphidae, leaving "copious and elaborate notes" in the collection (Pont, in litt.) as well as abbreviated annotations in copies of Walker's works and a copy of Kertész's catalog. These are apparently the "copious manuscript notes on Syrphidae, which he [Austen] made

some years ago in arranging the British Museum collection, and which have proved invaluable in my [Brunetti's] revisionary work" to which Brunetti (1923:v) refers. "There are two 'groups' of Austen labels. The first group, often exceedingly lengthy, gives discursive information on generic placings. These are the labels that have been 'discarded as knowledge and curation have progressed.' The second group includes labels that may say 'apparently seen by Walker, but differs from the description by characters a, b, c' or 'this is a male but Walker described a female.' Such labels are never discarded, as they are an integral part of the process of evaluating types or potential type material" (Pont, in litt.). Unfortunately, a number of Walker types have been lost with their notes (e.g., *Paragus fuscipennis, Eristalis anicetus, E. calida, E. jucunda, E. exterus, E. evers, E. transpositus, Helophilus grisea, H. hilaris, Milesia lamus,* etc.). Many of these types were present as late as 1955 as Ralph Coe, the curator then, indicated their location in the collection in a card file. However, I was not able to find them in 1974, 1984 nor 1987 and neither K. G. V. Smith nor Adrian Pont has been able find them.

Recently a red holotype label has been added to most Walker types that are now uniques (Fig. 10). This curatorial practice apparently stems from Crosskey (1974). However, there is no evidence in Walker's publications nor can it be demonstrated from evidence derived from outside those publications that these types are unique; they may merely be the sole surviving syntype of a series. Vane-Wright (1975) showed the fallacies of the "assumption-of-holotype" argument and the new Code has implemented Vane-Wright's position by stating that a holotype "can only be designated in the original publication and by the original author (art. 73(a) (iii)) and by making the publication of an "assumption of a holotype" a lectotype designation (ICZN, 1985, article 74b). Even so, it is unfortunate that the Diptera Unit of the British Museum has implemented a curatorial policy contrary to the recommendations of the Code (ICZN, 1985, recommendation 73F) and that assuredly will confuse future workers. In uniformity with the Code, I have designated all these unique types as lectotypes.

Wiedemann types are scattered among several museums, although most are in Vienna. Wiedemann indicated the location of the types of his species in their original descriptions. Those in his personal collection were purchased by Winthem when Wiedemann died in 1840. Winthem was apparently combining his collection with Wiedemann's when he, in turn, died in 1848. Both collections were later transferred to the Museum at Vienna (1852?) (q.v.). Until the late 1870's these collections were kept separate, but later were amalgamated when all the collections were moved to the new Museum. At that time, each specimen was labeled to indicate its origins either in the "Winthem" or "Wiedemann" collection, but as the collections had already been somewhat mixed by Winthem, Wiedemann types may have either a "Winthem" or a "Wiedemann" collection label (figs. 13, 17) (see Osten Sacken, 1878: xv–xvi).

The Naturhistorisches Museum at Vienna is one of the important depositories of types of early dipterists. While present collections are well curated, knowledge of the history of collections (Loew, 1856; Osten Sacken, 1878; Brauer, 1880) is essential to understanding these collections. The early collections were kept in the Hofburg, part of the imperial residence in Vienna. Unfortunately, during the revolution of 1848 parts of the collections were destroyed by fire. Thus, most of the types of the species

described from material from the "Wiener Museum" (Wiedemann) or "Kais. Königl. Museum" (Meigen) and perhaps that of "Hrn. Megerle von Mühlfeld" (Meigen) were probably destroyed. However, some of this material may have been in the Wiedemann and Winthem collections as Wiedemann was the intermediator between the Imperial Court and Meigen (Pont, 1986). The Wiedemann and Winthem collections came to Vienna after the fire and were maintained separately in boxes, as this is how Loew and Osten Sacken described them (Osten Sacken, 1878). A new natural history museum was built and the collections were moved to it in 1878–1880. At this time all the collections were amalgamated into drawers. The origin of the material was indicated by a special label: that from the general collection was labeled "Alte Samm- lung" (Fig. 12), from Wiedemann "Wiedemann Coll." (Fig. 13), and from Winthem "Winthem Coll." (Fig. 17). Material subsequently added to the collections does not have a special collection label.

adjuncta Walker, 1849:636 (*Volucella*). Type-locality: "––––?" Syntypes male & female BMNH. *Copestylum brunneum* (Thunberg). NEOTROPICAL: Puerto Rico and Virgin Islands.

Thompson (1981:129) identified this name as a junior synonym of *brunneum* Thunberg.

aenescens Macquart, 1842:59 (119) (*Eristalis*). Type-locality: "Patrie Inconnue" Type female ??? *Eristalinus aeneus* (Scopoli). HOLARCTIC: widespread; Hawaii; Tan- zania?

Macquart didn't indicate the location of his types in the original description. The type of *aenescens* Macquart was not found in Paris, London or Oxford. The descrip- tion indicates that this name applies to *Eristalinus aeneus* (Scopoli) as Macquart described the species as the same as *aeneus* except for black antennae and mesonotum without white vittae. These characteristics are typical of female *aeneus*. Kertész (1910: 210) listed the name as a questionable synonym of *aeneus*.

Agerinus Walker, 1849:608 (*Helophilus*). Type-locality: "––––?" Lectotype female BMNH. *Prohelophilus cingulata* (Fabricius). AUSTRALIAN: New Zealand.

A single female specimen with the appropriate Walker and Austen labels was examined and is designated lectotype. The specimen also bears a "New Zealand" locality label. This is a specimen of *Prohelophilus cingulata* (Fabricius) (new syn- onym), a common New Zealand species.

albohirta Wiedemann, 1830:110 (*Pipiza*). Type-locality: "Vaterland?" Lectotype male NMW. *Neocnemodon vitripennis* (Meigen). PALAEARCTIC: Europe.

A male with the appropriate Winthem label was examined (Fig. 17), is designated lectotype, and is a specimen of the common European species, *Neocnemodon vitri- pennis* (Meigen) (new synonym).

This name clearly illustrates the problem of *patria ignota* names. Delucchi and Pschorn-Walcher (1955) revised the European species of the genus *Neocnemodon* (as *Cnemodon*) as there was confusion as to how many species existed and what names to use for them. They indicated that the most commonly used name, *vitripennis* Meigen, had been applied to any or all of four different species. They characterized

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description. *Eristalis antidotus* Walker is a junior synonym of *arvorum*. As this assignment agrees with the original description, I accept the synonymy (new synonym).

Aquilius Walker, 1849:551 (*Eumerus*). Type-locality: "————?" Lectotype male BMNH. *Eumerus aquilius* Walker. AFROTROPICAL?

A single male specimen`with the appropriate Walker and Austen labels was examined and is designated lectotype. As I do not recognize this species, I am redescribing it and figuring its genitalia. As a *Eumerus* species, the type must be Old World in origin. I don't believe it represents a Palaearctic species as I did run it through Stackelberg's key (1961) including all subsequent modifications (Stackelberg, 1964, 1965; Peck, 1966) without success. I suspect the type represents an Afrotropical species as it is unlike any Oriental species I know.

Head: Black; face white pilose and pollinose; cheek white pilose and pollinose; frontal triangle small, about ¾ as long as eye contiguity, white pilose and pollinose, occiput white pilose and pollinose; vertical triangle large, about ⅔ as long as wide, black pilose, very sparsely gray pollinose except densely white pollinose anteriorly at eye contiguity. Eyes holoptic, white pilose, with eye contiguity long, about ⅓ as long as vertical triangle (Fig. 6). Antenna (Fig. 5) black, black pilose; third segment trapezoid, about ⅞ as long as wide; arista bare, black.

Thorax: Humerus white pilose and pollinose; mesonotum shiny except for broad lateral and narrow submedial gray pollinose vittae, with submedial vittae extending to scutellum, white and black pilose, with short black bristles dorsal to wing; scutellum shiny, white and black pilose, without a ventral fringe; pleurae subshiny, sparsely white pollinose, white pilose; sternopleural pile patches broadly separated. Wing: Hyaline; epaulet black, black pilose; microtrichose except for bare first costal cell, basal ⅕ of first basal cell, basal ¼ of second costal cell, basal ¼ of anal cell, and basal ½ of alula; third vein only slightly sinuate; stigma brown. Legs: Brownish black except for orange femoral-tibial joints and mid basitarsomere, extensively white pilose, black pilose only on apices of fore and mid femora, basal ½ of hind tibia, and hind tarsus; intermixed white and black pile on trochanters and apical ¼ of hind femur; hind femur slightly swollen, with ventral spines (Fig. 4).

Abdomen: Black; first three sterna gray pollinose, white pilose; fourth sternum shiny, black pilose; dorsum with shiny metallic lustre; first tergum sparsely grayish white pollinose, white pilose; second to fourth terga shiny except for submedial white pollinose lunulae, black pilose except white pilose laterally; genitalic segments shiny, black pilose. Male genitalia as figured (Figs. 1–3).

Bubulcus Walker, 1849:567 (*Milesia*). Type-locality: "————?" Lectotype male BMNH. *Criorhina bubulcus* (Walker). NEARCTIC: Pacific Northwest.

A single male specimen with the appropriate Walker and Austen labels was examined and is designated lectotype. This is a specimen of the common Pacific Northwest species now called *Criorhina luna* Lovett, new synonym.

caerulifrons Bigot, 1884:542 (*Xylota*). Type-locality: "Exot. Pays?" Holotype female BMNH. *Xylota caerulifrons* Bigot. HOLARCTIC: Palaearctic?

A single female specimen with the appropriate Bigot labels (Fig. 9) was examined.
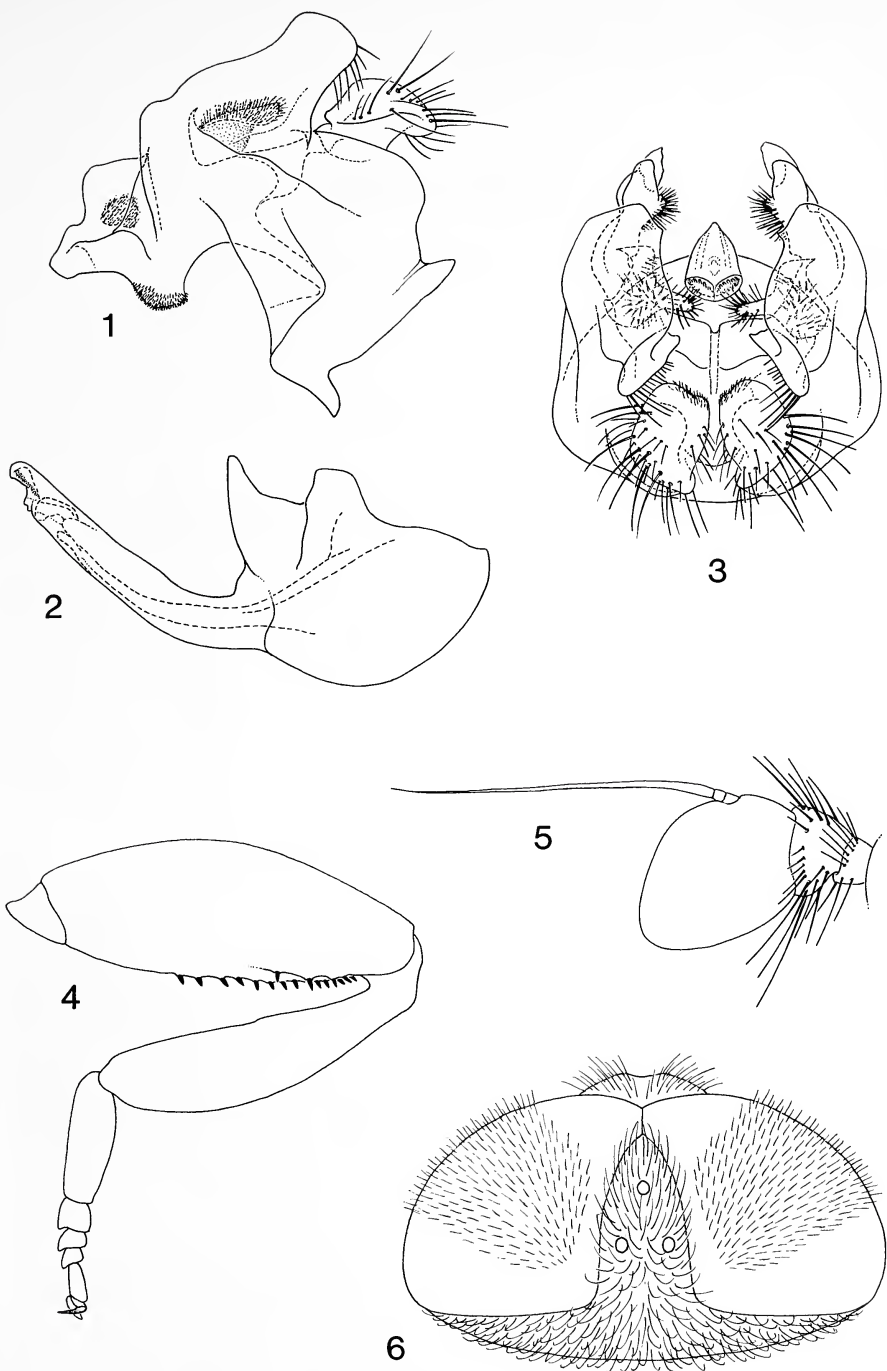
Figs. 1–6. *Eumerus aquilius* Walker. 1. 9th tergum and associated structures, lateral view. 2. 9th sternum and associated structures, lateral view. 3. 9th tergum and associated structures, dorsal view. 4. Hind femur, lateral view. 5. Antenna, lateral view. 6. Head, dorsal view.

The type is a specimen of *Xylota triangularis* group of Hippa (1968:189, 1978:65) and clearly represents a north-temperate species. Unfortunately, the taxonomy of the females of *Xylota* is poorly known. I do not believe the name applies to any Nearctic species.

calidus Walker, 1849:613 (*Eristalis*). Type-locality: "– – – – –?" Type(s) female BMNH. ? ??

No type was found in my searches during 1974, 1984 nor 1987. Austen apparently studied the type as he annotated a copy of Walker (1849) by changing "fem." to "mas." There is a card indicating that the type was present in 1955.

The original description is given below. Unfortunately, it includes no clues to generic placement of the name.

"*Eristalis calidus,* n. s., fem. Niger, scutello abdomineque fulvis hujus apice vittaque dilatata nigris, antennis piceis, pedibus flavo-fulvis, femoribus nigris, alis limpidis ad costam fulvis.

Body black; head covered with yellow down, clothed with yellow hairs; crown beset with a few black hairs; a broad brown shining stripe between the feelers and the mouth, which is pitchy; feelers pitchy; bristle tawny, downy; eyes pitchy; facets very small; chest and breast thickly covered with short tawny hairs; scutcheon tawny; abdomen nearly oval, tawny, longer and a little broader than the chest, clothed with short tawny hairs, black at the tip, and having on the back a black interrupted strip, which during its course is widened into two short bands; legs clothed with short tawny hairs; hips black; thighs black, with yellow tips; hind thighs pitchy, tawny towards the base; shanks tawny, yellow at the base; feet pitchy, tawny towards the base; claws and foot-cushions tawny; tips of claws black: wings colourless, tawny along the fore border for more than half the length, where there is a small brown spot; wing-ribs tawny; veins black, tawny towards the base; poisers yellow. Length of the body 6 lines; of the wings 12 lines."

caliginosus Walker, 1849: 621 (*Eristalis*). Type-locality: "– – – – –?" Lectotype female BMNH. *Palpada caliginosa* (Walker). NEOTROPICAL: Bolivia?

A single headless female specimen with the appropriate Walker and Austen labels was examined and is designated lectotype. The specimen belongs to the genus *Palpada* (sensu stricto or *scutellaris* group of Thompson 1981:149) (new combination) and is similar to *aemulus* Williston. The type represents a species unknown to me, but a male from Bolivia (Buena Vista, April) from the Melander Collection (USNM) appears to belong to the same species. The following is a description of the lectotype.

Thorax: Black; black pilose except gray pollinose and yellow pilose anterior to transverse suture; scutellum black on basal ⅓, yellow apically, black pilose; pleurae gray pollinose, yellow pilose except pteropleuron black pilose; metasternum yellow pilose; squama brown with white fringe. Wing: Hyaline, microtrichose apically; bare anterobasally to Rs, basal ⅔ of 1st basal cell, underspurious vein in 1st basal cell, 2nd basal and anal cells, posterior to anal cell, cubital cell except medially, and alula except along basal margin. Legs: Black except orange femoral-tibial joints, black pilose except yellow pilose on coxae and dorsally and ventrally on hind femur; coxae gray pollinose.

Abdomen: Black except large orange quadrate basolateral macula on 2nd tergum, dull black pollinose except on orange maculae and for shiny mediate fasciate maculae on 3rd & 4th terga, black pilose except for yellow pile on 1st and basolaterally on all other terga.

chalybea Wiedemann, 1830:98 (*Xylota*). Type-locality: "Vaterland?" Lectotype male NMW. *Chalcosyrphus violascens* (Megerle). NEARCTIC: Eastern North America.

Two headless males were studied. One male had "Coll. Winthem" and Curran type label, and the other had an "Alte Sammlung" label. As the type was stated to be "Im Wiener Museum," I have selected the male with the "Alte Sammlung" label as lectotype. Both types are specimens of the common Eastern North American species, now called *chalybea.*

Osten Sacken (1875:60) first correctly identified this name as applying to a common Nearctic species. Curran (1926:114) reported on the status of the type specimen. See under *violascens.*

coactus Wiedemann, 1830:165 (*Eristalis*). Type-locality: "Vaterland?" Lectotype male NMW. *Mallota posticata* (Fabricius). NEARCTIC: Eastern North America.

Two males were studied. The male with Curran's determination label is designated lectotype. Both specimens are representatives of the common Eastern North American species, *posticata* Fabricius.

Osten Sacken (1878:135) first correctly identified this name as applying to a common Nearctic species. Curran (1930b: 2) reported on the status of the type specimen.

Coenina Walker, 1849:560 (*Milesia*). Type-locality: "-----?" Lectotype female BMNH. *Milesia crabroniformis* (Fabricius). PALAEARCTIC: Southern Europe, Caucasus, Madeira.

A single female with the appropriate Walker and Austen labels was examined and is designated lectotype. This specimen is also labeled with "Madeira" in a hand unknown to me.

Austen synonymized this name under *Milesia crabroniformis* (Fabricius) in his copy of Kertesz, and I confirm his identification (new synonym).

coerulescens Macquart, 1834:519 (*Senogaster*). Type-locality: "Exotique" Type? male UMO *Semogaster dentipes* (Fabricius). NEOTROPICAL: Surinam to Brazil.

A male with the appropriate Macquart label was studied in Oxford and is a specimen of the species *dentipes* Fabricius. This is probably not the type, but the second specimen reported by Macquart. No other material was found in Paris or London.

Macquart (1842:72) reported a second specimen of his species from Surinam (collection of Serville). Williston (1886:321) placed the name as a questionable synonym of *dentipes* Fabricius and all subsequent authors have accepted his synonymy.

copiosus Walker, 1852:249 (*Eristalis*). Type-locality: "-----?" Lectotype male BMNH. *Eristalinus copiosus* (Walker). AUSTRALIAN: Australia.

A single female specimen with the appropriate Walker name and type and Austen labels was examined and is designated lectotype. This is a specimen of *sinuata*

Thomson. Klocker (1924:57) first identified this name with an Australian species. Later Ferguson (1926:161, 518) synonymized it with *sinuata* Thomson.

Corbulo Walker, 1849:556 (*Xylota*). Type-locality: "—————?" Lectotype female BMNH. *Xylota florum* (Linnaeus). PALAEARCTIC: Europe and Siberia.

A single female specimen with the appropriate Walker and Austen labels was examined and is designated lectotype. This is a specimen of the Palaearctic species *Xylota florum* Linnaeus (new synonym).

corolloides Macquart, 1850:156 (*Syrphus*). Type-locality: "Patrie inconnue" Syntypes male & female *Eupeodes* (*Metasyrphus*) species HOLARCTIC?

Macquart did not indicate the location of his types in the original description. The types of *corolloides* Macquart were not found in Paris, London or Oxford. The description suggests that this name applies to a species of the *latifasciatus* group of the subgenus *Metasyrphus* of *Eupeodes* (new combination).

costalis Wiedemann, 1830:97 (*Baccha*). Type-locality: "Vaterland?" Lectotype male NMW. *Ocyptamus costatus* (Say). NEARCTIC: Eastern North America.

A male labeled "F.," "costalis, Alte Sammlung" and with a Curran type label was examined and is designated lectotype. It is a specimen of *costatus* Say.

Curran (1926:113) identified *costalis* as the same as *tarchetius* Walker and later (Curran 1930a:6) identified both of these names as synonyms of *Baccha costata* Say.

cyaneifer Walker, 1849:621 (*Eristalis*). Type-locality: "—————?" Type(s) ? BMNH. *Palpada scutellaris* (Fabricius). NEW WORLD: United States south to Argentina.

No type specimen was found in my searches during 1974, 1984 or 1987. Also, there is no card for this name in the type specimen file. The name was identified as a synonym of *Palpada scutellaris* (Fabricius) by Kertész (1910:235). As the description of *cyaneifer* does fit *scutellaris,* I accept Kertész's synonymy.

Daochus Walker, 1849:565 (Milesia). Type-locality: "————?" Lectotype female BMNH. *Temnostoma daochus* (Walker). NEARCTIC: Southeastern North America.

A female specimen with the appropriate Walker and Austen labels was studied and is designated lectotype. This specimen is of the species previously called *Temnostoma pictulum* Williston (new synonym), a common southeastern United States species.

Dascon Walker, 1849:554 (*Xylota*). Type-locality: "—————?" Lectotype male BMNH. *Chalcosyrphus metallicus* (Wiedemann). NEARCTIC: Southeastern North America.

A male with the appropriate Walker and Austen labels was examined and is designated lectotype. The type is a representative of the southeastern United States species, *Chalcosyrphus metallicus* (Wiedemann) (new synonym).

Shannon (1926:21) suggested that *dascon* was a synonym of *nemorum* Fabricius. The hind legs of the type are much darker than those of typical *metallicus* specimens,

and this may have misled Shannon. However, I dissected the male genitalia of the type and found them to be typical of *metallicus.*

Datamus Walker, 1849:628 (*Eristalis*). Type-locality: "–––––?" Lectotype female BMNH. *Phytomia zonata* (Fabricius). PALAEARCTIC & ORIENTAL: Japan and Manchuria, south to India and southeast Asia.

A single female specimen from the Children's collection, with the appropriate Walker and Austen labels, was examined and is designated lectotype. This name was synonymized with *Phytomia zonata* (Fabricius) by Austen (in Brunetti 1923:204).

decora Walker, 1849:553 (*Syritta*). Type-locality: "–––––?" Lectotype female, BMNH. *Syritta decora* Walker. AFROTROPICAL: Mauritius.

A single female specimen with the appropriate Walker and Austen labels was studied and is designated lectotype.
Smith and Vockeroth (1980:507) identified this name as applying to an Afrotropical species known only from Mauritius.

dibaphus Walker, 1849:560 (*Xylota*). Type-locality: "–––––?" Lectotype female BMNH. *Senaspis dibapha* Walker. AFROTROPICAL: Guinea-Bissau to Kenya, south to Mozambique.

A single headless female with the appropriate Walker type labels was studied and is designated lectotype. This name was first identified by Austen (in Bezzi 1915:62).

dives Walker, 1849:617 (*Eristalis*). Type-locality: "–––––?" Lectotype male BMNH. *Eristalinus dives* (Walker). AUSTRALIAN: Fiji and Samoa.

A single headless male with the appropriate Walker and Austen labels was studied and is designated lectotype.
The type is a specimen of *Eristalinus* (new combination) and agrees well with a male determined as *nitidus* Wulp from Fiji (Bezzi, 1928:79) in the BMNH collections. However, the name represents a species distinct from *nitidus* of Wulp, which was described from Java, as its abdomen lacks the characteristic sinuate black pollinose fasciae of *nitidus.* Hull (1929:198) also recorded this species from Samoa as *nitidus,* and described it from Fiji as *vitrescens* Hull (new synonym).

dubia Macquart, 1834:507 (*Eristalis*). Type-locality: [none given] Type ? Macquart Collection. ???

No specimens labeled as *dubia* Macquart were found in Oxford, London or Paris nor is any material listed as being present in the Macquart Collection in Lille. The original description is translated below. Macquart's placement in *Eristalis* and other key characters place the name in the subtribe Eristalina and among genera related to *Eristalis.* The banded thorax is suggestive of a New World *Palpada* species, but the swollen hind femur with a "tooth" is a character not known for any *Palpada* species.
Length 13.5 mm. Blackish. Face whitish; prominence tawny. Front tawny. Antennae tawny. Thoracic pile yellowish; a transverse band on anterior border; another similar one to this on posterior border yellowish; scutellum testaceous. Second seg-

ment of abdomen with a large interrupted tawny band; posterior border shiny white, as are those of following segments. Legs brown; base of tibiae yellowish; hind femur swollen and provided with a tooth. Wings brownish. This species, of my collection, is intermediate between *Eristalis* and *Helophilus*.

From Macquart's key, the following additional characters can be adduced for *dubia*: arista bare, marginal cell (R1) closed and petiolate, and eyes bare.

erraticum Walker, 1849:543 (*Chrysotoxum*). Type-locality: "————?" Lectotype female BMNH. *Callicera erratica* (Walker). NEARCTIC: Eastern North America.

A single female with the appropriate Walker and Austen labels was studied. Verrall (1913:329) transferred this name to *Callicera* and redescribed the type. Thompson (1980:201) recognized the name as the senior synonym for the Nearctic species, *Callicera johnsoni* Metcalf, and designated the lectotype.

fascipennis Wiedemann, 1830:96 (*Baccha*). Type-locality: "Vaterland?" Lectotype female NMW. *Ocyptamus fascipennis* (Wiedemann). NEARCTIC: Eastern North America.

A female labeled "Am. Bor.," "aurinotus, = fascipennis, Alte Sammlung," "type, Baccha, fascipennis Wd., No. CNC [Red CNC type label]" was studied. Osten Sacken (1875:50) first identified this name as applying to a Nearctic species when he listed it as a questionable synonym of *aurinota* Walker. Later he (1878:127) removed the question mark. While he never commented on his synonymy, it was undoubtedly the result of having studied the type in Vienna. The type was then in a separate collection as noted above. The "Am. Bor." and "aurinotus = fascipennis" were added to the type after Osten Sacken studied it and probably on the basis of his identification. Curran (1926:123) reexamined the type and confirmed Osten Sacken's synonymy. The specimen is here designated as lectotype and is so labeled.

flavicornis Macquart, 1842:71 (*Merodon*). Type-locality: "Nous la croyons exotique." Holotype male MNHNP. *Merodon aureus* (Fabricius). PALAEARCTIC: Europe and North Africa.

In the Macquart collection in Paris, a headless male labeled as "No. 1184, Merodon flavicornis" was studied. This holotype is a specimen of *Merodon aureus* (Fabricius) (new synonym).

fumipennis Stephens, 1846:29 (*Eristalis*). Type-locality: "I am not aware of its locality." Holotype male BMNH (lost?). *Palpada geniculata* (Fabricius). NEOTROPICAL: Surinam to Brazil.

The original description and figure of *fumipennis* was included in Stephens' "British Insects . . .", although Stephens plainly was unaware of its locality. Walker (1851: 243) merely redescribed the species in his *Insecta Britannia, Diptera*. The holotype of *fumipennis* Stephens should be in the Stephens Collection now in the British Museum. However, the type has apparently been lost since Verrall's time (Verrall, 1901:672). Haliday (in Walker, 1856:xii) suggested that the specimen belonged to the species *Palpada vinetorum* (Fabricius). Verrall (1901:672) examined the type, gave further descriptive details, and suggested that the name applied to *Palpada hortorum* (Fabricius) (Bezzi and Stein, 1907:100). However, the original description

and color figure suggest that this name applies to *Palpada geniculata* (Thompson et al., 1976:106).

fusca Macquart, 1834:495 (*Volucella*). Type-locality: "Exotique" Holotype female UMO. *Copestylum brunneum* (Thunberg). NEOTROPICAL: Puerto Rico and Virgin Islands.

This name was based on a female from the Serville Collection. There is a single headless female labeled as "V. fusca, Coll. Serville Macq." in the Bigot-Verrall-Collin Collection at Oxford. The Diptera from the Serville Collection were purchased by Bigot as Osten Sacken (1878:xvi) stated that the types from the Serville Collection are to be found in the Bigot Collection. The type is a specimen of *Copestylum brunneum* (Thunberg), a common Antillean species (new synonym).

fuscipennis Walker, 1849:545 (*Paragus*). Type-locality: "–––––?" Type(s) male BMNH. *Pipizella viduata* (Linnaeus)?. PALAEARCTIC: Europe.

The type was not found in 1974 nor 1984 in the BMNH, but there was a card indicating that the type was present in 1955. Austen apparently studied the type as he annotated a copy of Walker (1849) with "A dark-winged *Pipizella virens,* F." Austen's identification is reasonable at the generic level, but in his time *virens* was not recognized as the species complex it is now known to be (Collin, 1952; Goeldlin, 1974; Lucas, 1976). As the species of the complex are recognized only on the basis of male genitalic characters, without examining the type of *fuscipennis* the name can not be identified with certainty and is here listed as a dubious synonym of *viduata* Linnaeus (new synonym), the oldest name in the complex.

fusciventris Wiedemann, 1830:95 (*Baccha*). Type-locality: Vaterland? Lectotype female NMW. *Pseudodoros clavata* (Fabricius). NEW WORLD: California to New Jersey, south to Argentina.

A female labeled with "F.," "fusciventris, Alte Sammlung" and with Curran type and determination labels was examined, is designated lectotype and is a specimen of *clavata* Fabricius.
Curran (1926:113) examined the type and identified it as "a rather discolored specimen of . . . *clavata* (Fabricius)."

Gerstaeckeri Becker, 1894:477 (*Chilosia*). Type-locality: "Vaterland?" Holotype; female ZMHU, Berlin. *Cheilosia gerstaeckeri* Becker. PALAEARCTIC: Sweden.

Gaunitz (1963:497) recorded this species from Sweden, Ammarnas.

haesitans Walker, 1849:615 (*Eristalis*). Type-locality: "–––––?" Lectotype female BMNH. *Eristalis dimidiatus* Wiedemann. NEARCTIC: Eastern North America.

A single female specimen with the appropriate Walker and Austen labels was examined and is designated lectotype. This is a specimen of *Eristalis dimidiatus* Wiedemann (new synonym).

hilaris Walker, 1849:605 (*Helophilus*). Type-locality: "–––––?" Type(s) ? BMNH. *Mesembrius hilaris* (Walker). AUSTRALIAN: New Guinea, south to Australia (Queensland, New South Wales).

In 1974 and 1984, I was unable to find the type, although there was a card indicating that it was present in 1955.

Edwards (1915:409) studied the type and identified this name with an Australian species. Ferguson (1926:165) contrasted the species with *bengalensis* Wiedemann (1819:16) and gave additional distributional records.

involvens Walker, 1860:291 (*Eristalis*). Type-locality: "————" Lectotype female BMNH. *Palpada furcata* (Wiedemann). NEW WORLD: Texas to Argentina.

A single female with the appropriate Walker and Austen labels was studied. The specimen consists of the head of one species (a female *Eoseristalis*) glued on to the body of a *Palpada furcata* (Wiedemann) (new synonym). I designate the body as lectotype.

jucundus Walker, 1849:620 (*Eristalis*). Type-locality: "—————?" Type(s) female BMNH. *Eristalinus* (*Eristalodes*) *quinquelineatus* (Fabricius). AFROTROPICAL: Cape Verde Islands to Ethiopia, south to South Africa.

In 1974 and 1984, I was unable to find the type, although there was a card in the type file indicating that it was present in 1955. Austen left a footnote in a copy of Walker (1849) referring to "clothed with black hairs only on the hind tibiae, and at the tips of the hind femora, underneath. E. E. A."

The original description gives the eyes as with "four black stripes," which clearly restrict the name to an *Eristalinus* (*Eristalodes*) species, and other characters, such as the black facial and mesonotal vittae, place the name as a synonym of *quinquelineatus* Fabricius (new synonym).

Lamus Walker, 1849:562 (*Milesia*). Type-locality: "—————?" Syntypes females BMNH. ? ??

In 1974, 1984 and 1987, I was unable to find the types. There is no card for it in the type file nor did Austen leave any annotations about it.

The original description is given below, and is of either a *Milesia* or *Spilomyia* species or both. The description of the eyes as "varied with dark red" is characteristic of *Spilomyia,* but I know of no *Spilomyia* species with the thorax or abdomen like that described for *lamus.* Those parts of the description seem to apply to a species of *Milesia,* such as *virginensis* Drury. This may mean that the description was based on a composite, a head of a *Spilomyia* species and the body of a *Milesia* species, and, as both Walker and Macquart have been known to describe such monstrosities, such is a likely possibility in this case.

"*Milesia Lamus,* n. s., fem. Flava nigro varia, abdomine fulvo, basi fasciis vittisque nigris, antennis fulvis, pedibus fulvis, tibiis posticis ferrugineo vittatis, femoribus posticis tarsisque ferrugineis, alis cinereis ad costam fuscis.

Head yellow, with a black band across the crown, whence a black strip extends to the base of the feelers; the latter are seated on a brown space, and a tawny strip proceeds from them to the clypeus; mouth pitchy; feelers bright tawny; third joint nearly round; bristle about thrice its length, pitchy towards the tip; eyes coppery, varied with dark red; facets small; chest yellow, adorned with a square black spot on each side of the front, and with a black strip along the middle joining a black

band between the wings; another black band occupies the fore border of the scutcheon; breast black, yellow in front, and adorned with two yellow spots on each side; abdomen tawny, black at the base, adorned with two slender black bands along the fore borders of the segments; a black stripe extends from the base along half the length of the following segment, and thence passes to the sides of the abdomen by means of two slender slightly curved and retreating bands; another black stripe springs from the black suture of the following segment, but is much shorter than the first, and the bands in which it terminates are nearly straight; the third black suture does not emit a stripe, but from it proceed two black bands, which are oblique and irregular in their course to the sides of the abdomen; underside yellow, with a large black spot in the middle of each segment, and brown spot on each side of its hind border; legs tawny; feet ferruginous, pitchy towards the tips; claws and foot-cushions yellow, tips of claws black; hind legs ferruginous, their shanks tawny, with ferruginous stripes; wings gray, brown along the fore borders for about half the breadth where the two colours are intermingled; wing-ribs tawny; veins pitchy, ferruginous along the fore border, tawny in the disk; poisers yellow. Length of the body 9 lines; of the wings 16 lines.

Var. B. Scutcheon black, excepting the hind border: wings gray, tinged with brown along the fore border for one-third of the breadth."

laphriaeformis Walker, 1849:558 (*Xylota*). Type-locality: "––––––?" Lectotype female BMNH. *Brachypalpus laphriformis* Fallén. PALAEARCTIC: Europe.

A single female specimen with the appropriate Walker and Austen labels was studied and is designated lectotype. Coe (1941:195) examined the type and synonymized the name under *bimaculatus* Macquart. The senior name for *bimaculatus* is *laphriformis* Fallén.

latus Macquart, 1842:35 (*Eristalis*). Type-locality: "Patrie inconnue" Holotype female Macquart Collection. *Phytomia zonata* (Fabricius). PALAEARCTIC and ORIENTAL: Korea and Japan, south to India and Southeast Asia.

The type was not found in the Macquart collection in Paris nor among the Macquart material in Oxford and London.

While this species was described from an unknown locality, Macquart (1846:126) later recorded a specimen from India, and, hence, both Wulp (1896:114) and Kertész (1910:223) listed this name as a valid Oriental species. Brunetti (1923:192) gave a translation of the original description. Herve-Bazin (1923:253) listed the name as a synonym of *zonata* without explanation. Macquart's figure is atypical for *zonata* as the pale fascia on the second tergum is broadly interrupted medially and the wing is more extensively dark. However, the figure does agree with a *zonata* specimen in the USNM from Java. Hence, Herve-Bazin's synonymy is here accepted.

lepida Macquart, 1842:109 (*Baccha*). Type-locality: "Patrie inconnue" Lectotype male, MNHNP. *Ocyptamus lepidus* (Macquart). NEOTROPICAL: Mexico south to Brazil.

Thompson (1981:53, 192) discussed the identity of this name, differentiated the species from related ones and designated a lectotype. *Lepidus* of Curran (1930a:3,

1941:262) and other recent authors is *ricus* Curran, and *crocatus* Austen is the true *lepidus* Macquart.

linearis Walker, 1852:251 (*Volucella*). Type-locality: "-----?" Lectotype female BMNH. *Volucella linearis* Walker. PALAEARCTIC: Japan.

A single female with the following labels was studied: "type" (green Walker type label), "Locality?, A. R. Wallace, ex. coll., W. A. Saunders, 68.4," "68.4," "Volucella, linearis" (in Walker's hand), "Volucella, linearis, Wlk" (Austen Label), and "head probably not belonging to body, owing to rapid narrowing of frons. Sp. trifasciata W. t. E. B." [=teste Enrico Brunetti] (in Brunetti's hand) (Figs. 10, 16). Brunetti (1923:147) listed this name as a synonym of *trifasciata* Wiedemann and stated that the type was "labeled as from India." However, I found no such label on the type. The type is a specimen of *nitobei* Matsumura (new synonym) and is designated lectotype.

longirostris Macquart, 1846:124 (*Volucella*). Type-locality "Patrie inconnue" Holotype female UMO. *Copestylum longirostre* (Macquart). NEOTROPICAL: Chile.

A single female with a bordered Bigot label ("V. longirostris o, am. mer. chili, (Coll. Fairmaire) Macq. D. ex.") was studied in the Bigot-Verrall-Collin collection at Oxford. This type is a specimen of the species previously called *concinna* Philippi (new synonym).

neglectus Wiedemann, 1830:134 (*Syrphus*). Type-locality: "Vaterland?" Syntypes males & females KIEL & NMW. ? ?

Type material, which minimally must have consisted of 3 males and a female, was not found in either Copenhagen or Vienna and is presumed to be lost. Rondani (1875: 423; Wulp, 1896:119) identified this name with a species from Sarawak, Borneo.

Wiedemann's original description has been translated below.

Black, thoracic sides, scutellum, abdominal bands except black interruptions, antenna and legs yellow. 7.6 mm

Antenna reddish yellow; face pale yellow, with slight pearlmother shimmer; frons on the sides yellow, middle bluish. Thoracic sides metallic blackish, with pale yellow bands and spot on its end; mesonotum black. First abdominal segment on the base and sides yellow, on the tip black, so that the yellow appears twice sinuate; second segment on the base hardly very narrowly yellow, but on the middle with rather broad and complete band, and one small triangular spot on the tip; each following segment on the base with very broad, on hindmargin outwards to both sides narrowed band, which in the front encircles a black transverse line, which bends backwards next to the middle on both sides, so that a yellow stripe seems to grow out of the middle of the band. The yellow stripe is fused with a band of the tip that is much narrower and with more shortened sides. These black lines on some male examples are very faint, but still present. Wing very waterclear [=*wasserklar*].

oxycanus Walker, 1852:246 (*Eristalis*). Type-locality: "----?" Lectotype male BMNH. *Helophilus groenlandicus* (O. Fabricius). NEARCTIC: Alaska to Greenland, south to British Columbia, Colorado and New Hampshire.

A single male with the appropriate Walker and Austen labels was studied and is designated lectotype. This is a specimen of *Helophilus groenlandicus* (Otto Fabricius) (new synonym).

peas Walker, 1849:590 (*Syrphus*). Type-locality: "–––––?" Type male BMNH. *Ocyptamus fuscipennis* (Say). NEARCTIC: Eastern North America.

Austen (1893:134) identified this name as the same as *fuscipennis* Say.

pictus Macquart, 1846:130 (*Eristalis*). Type-locality: "Patrie inconnue" Holotype female ?. *Meromacrus acutus* (Fabricius). NEARCTIC: Southeastern United States.

Described from a single female labeled as "Pictus, Leach" and in the collection of Latreille which was stated as being maintained by the Marquis of Breme. The type was not found in the Macquart Collection in Paris nor among the Macquart material in Oxford and London. Horn and Kahle (1935:150) stated that Latreille's first collection went to P. F. M. A. Dejean in 1826 and that his second collection was broken up after his death and distributed among numerous people. They did not indicate where the Diptera of this second collection went. Latreille died in 1833. The first statement corresponds to what Macquart (1838:12) wrote at the beginning of his work. Later Macquart (1846:130, 132) wrote that the Latreille material was now with (*actuellement*) or maintained (*maintenat*) by "M. de Marquis de Breme." This last reference must then refer to the results of the break-up of this second collection. Unfortunately, Horn and Kahle (1935:29) gave no indication of what happened to the Diptera material of Breme as they only noted that the Coleoptera went to the Zoological Museum in Turin. Also, there is a brief announcement in the *Bulletin de la Société Entomologique de France* (1850, 2nd series, 8:xix) stating that Breme donated his collection of insects to the museum in Turin. However, I have not been able to verify that there are Macquart Diptera types in Turin.

The name clearly applies to a *Meromacrus* species, of the *pratorum* complex. In the most recent key to this complex (Thompson, 1981), the character states of orange base of the wing and black facial vitta identify the name as a synonym of *acutus* Fabricius.

purpurea Walker, 1849:560 (*Xylota*). Type-locality: "––––?" Lectotype female BMNH. *Chalcosyrphus violascens* (Megerle). NEARCTIC: Eastern North America.

A single female with the appropriate Walker and Austen labels was studied and is designated lectotype. This name was first identified as a synonym of *chalybea* by Shannon (1926:16). See *violascens*.

quadrivittatus Wiedemann, 1819:17 (*Eristalis*). Type-locality: " " Holotype male NMW. *Mesembrius quadrivittatus* (Wiedemann). ORIENTAL: India, Indonesia (to Aru Islands).

Wiedemann (1819) did not formally describe this species; he merely contrasted it with the preceding one (*Mesembrius bengalensis* [Wiedemann]), stating that he was doubtful whether the unique male was distinct. In his monograph (Wiedemann 1830: 168), he merely removed his statement of doubt, calling this species similar to the preceding (again *bengalensis*), and repeating his statements of differences from the original description. As Wiedemann never made a formal description, the lack of

locality data for *quadrivittatus* was either an oversight (see under *xanthaspis*) or he meant to cover it under his expression that *quadrivittatus* was "*vorigen ausserst ähnlich . . .*" The latter possibility is confirmed by the fact there is a male from the Winthem Collection determined by Wiedemann as *quadrivittatus* and labelled as being from Bengal (the type locality of *bengalensis*). This specimen has a small pink square indicating that it is a type (see Osten Sacken 1878:xv). What is curious about this specimen, is that Curran (1930b:1) stated that it is not the holotype "as the type locality is Tranquebar, while the specimen [=the holotype] before me is from Bengal." As I have found no basis whatsoever for Curran's assertion, I accept the specimen as holotype, making the type locality Bengal.

rufitarsis Macquart, 1842:58 (*Eristalis*). Type-locality: "Patri inconnue." Holotype female MNHNP. *Phytomia zonata* (Fabricius) PALAEARCTIC & ORIENTAL: Japan, Korea, south to India and Southeast Asia.

Two females are in the Macquart Collection (Box 16, #634) under this name, but only one is labeled. The female with a Macquart label is considered the holotype and is a specimen of the common widespread Far East species, *Phytomia zonata* (Fabricius) (new synonym). The other is a specimen of *Phytomia aesymnus* Walker.

secretus Walker, 1849:620 (*Eristalis*). Type-locality: "----?" Lectotype ? BMNH. *Eristalinus taeniops* (Wiedemann). PALAEOTROPICS: Southern Europe, east to India and south to South Africa.

Only a fragment of a type remains, consisting of a thorax, left mid leg, all legs on right side and abdominal terga 1–4. The fragment is also badly rubbed and discolored. It is designated lectotype. However, the fragment is clearly a part of specimen of *Eristalinus* and probably *taeniops* Wiedemann (new synonym).

solennis Walker, 1849:245 (*Eristalis*). Type-locality: "----?" Lectotype male BMNH. *Palpada solennis* (Walker). NEW WORLD: Texas south to Argentina.

A single male with the appropriate Walker and Austen labels was studied and is designated lectotype. Thompson et al. (1976:109) identified this name as the senior synonym for *mus* Curran, a Neotropical species.

stipatum Walker, 1852:219 (*Chrysotoxum*). Type-locality: "---?" Lectotype female BMNH *Chrysotoxum intermedium* (Meigen). PALAEARCTIC: Europe, North Africa.

→

Figs. 7–11.   Labels. 7. *Helophilus rostratus* Macquart: a—the Macquart name label glued onto a Bigot label, b—Verrall donation label, c—type label with red circle. 8. *Eristalis oxycanus* Walker: a—Austen name label, b—Walker type with green circle, c—Walker name label. 9. *Xylota caerulifrons* Bigot: a—Verall donation label, b—holotype label with red circle, c—Bigot name label. 10. *Volucella linearis* Walker: a—Austen name label, b—Walker type with green circle, c—Walker name label, d—locality label of unknown origin, e—BM acquisition number, f—holotype label with red circle. 11. *Merodon angustiventris* Macquart: a—Macquart name label, b—Thompson paralectotype label yellow in color, c—ex coll Bigot label, d—Austen name label?, e—cotype label with yellow circle, f—BM acquisition.

7

*Holophilus
rostratus
n. sp.
nov.Granata.   mag. & ex.hom*

ex.coll.Bigot.
Prs by
G.H.Verrall.
B.M.1901-14.

Type

8

*Eristalis
oxycanus,Wlk.*

Type

oxycan·e

9

ex.coll Bigot.
Pres. by
G.H Verrall.
B.M.1894-234.

Holo-
type

X. Caerulifrons. ♀

10

*Volucella
linearis
Wlk.*

Type

Holo-
type

*Locality?
A.R Wallace
coc coll
W.W. Saunders.
1.8.4.
63.4*

11

*Merodon
angustiventris
Meica.*

PARALECTOTYPE
angustiventris Mag
desgn. Thompson 1978

Co-
type

Ex coll: Bigot.

*Merodon
angustiventris
1/acq.*   *B.7.1901·14*

A single female with the appropriate Walker and Austen labels was studied and is designated lectotype. Austen identified the type as a specimen of *italicum* Rondani, a name that is now considered synoymous with *intermedium* (Meigen). I accept this synonymy (new synonym).

strenuus Walker, 1857:152 (*Helophilus*). Type-locality: [none given] Lectotype male BMNH. *Mesembrius strenuus* (Walker). PALAEOTROPICS.

A male with the appropriate Walker and Austen labels was examined and is designated lectotype. The type is a specimen of *Mesembrius* unknown to me (new combination).

tenebricus Walker, 1849:601 (*Merodon*). Type-locality: "----?" Lectotype female BMNH. *Palpada furcata* (Wiedemann). NEW WORLD: Texas to Argentina.

A single female with the appropriate Walker and Austen labels was studied and is designated lectotype. Shannon and Aubertin (1933:161) first identified this name as the same as *furcata* Wiedemann.

tomentosus Macquart, 1850:140 (*Eristalis*; preocc. Macquart, 1847). Type-locality: "Patrie inconnue." Lectotype female NMNHP. *Palpada mexicana* (Macquart). NEW WORLD: California to Texas, south to Venezuela and Peru.

In Box 16, #641 of the Macquart Collection in Paris, there are two specimens associated with this name. The female with a Macquart label "Eristalis, tomentosus, Macq. n. sp." is designated lectotype and has been so labeled. Both specimens are of *Palpada mexicana* (Macquart) (new synonym).

torpidus Walker, 1857:153 (*Merodon*). Type-locality: [none given]. Lectotype male BMNH. *Orthoprosopa grisea* (Walker). AUSTRALIAN: Australia.

A male with the appropriate Walker and Austen labels was examined and is designated lectotype. The type is a specimen of *Orthoprosopa grisea* (Walker) (new synonym).

torridus Walker, 1849:612 (*Eristalis*). Type-locality: "----?" Lectotype female BMNH. *Eristalinus taeniops* (Wiedemann). PALAEOTROPICS: Southern Europe, east to India and south to South Africa.

A single headless female with the appropriate Walker and Austen labels was studied and is designated lectotype. Yerbury (in Verrall 1898:415) identified this name as a synonym of *taeniops* Wiedemann.

varia Walker, 1849:548 (*Baccha*). Type-locality: "---?" Syntypes male(s) and female(s) BMNH. *Pseudodoros clavatus* (Fabricius). NEW WORLD: California to New Jersey, south to Argentina.

Austen (1898:159) identified this name as a synonym of *clavatus* Fabricius.

violascens Megerle, 1803:[36] (*Syrphus*). Type-locality: "Exotica" Lectotype female NMW. *Chalcosyrphus violascens* (Megerle). NEARCTIC: Eastern North America.

The description of this species appeared in a sales catalog prompting the question of whether the name is available. Two other Diptera names also appeared in the same catalog, and one of these, *Hippobosca variegata,* is currently accepted as avail-

Figs. 12–17. Labels. 12. *Volucella maximiliani* Jaennicke: a—locality label, b—Alte Samm-lung label, c—Jaennicke label?. 13. *Paragus politus* Wiedemann: a—NMW old determination label, b—Winthem Collection label, c—Wiedemann name label. 14. *Xylota laphriaeformis* Walker: a—Walker type label with species name in Austen's hand, b—BM acquisition label, c—locality label of unknown origin, d—Austen name label. 15. *Musca gibba* Fabricius: a—Fabricius name label, b—Sehested & Tonder Lund label. 16. *Volucella linearis* Walker: a—Brunetti comment label. 17. *Pipiza albohirta* Wiedemann: a—Winthem Collection label, b—Delucchi determination label.

able (Maa, 1963:131, 1969:286; Crosskey, 1980:1077) from that catalog. Wiedemann (1830:581 & 603) had recognized both of them (*Pygrota undulata* and *Hippobosca variegata*) as available from Megerle. Hence, I also accept *violascens* as an available name. The description clearly identifies this name as applying to the species presently known as *Chalcosyrphus chalybeus* (Wiedemann)(new synonym). Wiedemann based his name on an unlabeled specimen in the Vienna Museum. I suspect that the type of *chalybeus* Wiedemann is in fact the type of *violascens* Megerle and so designate it as lectotype. Wiedemann clearly had access to Megerle's material as he redescribed two other Megerle species.

vittatum Wiedemann, 1830:87 (*Chrysotoxum*). Type-locality: "Vaterland?" Lectotype female NMW. *Sphecomyia vittata* (Wiedemann). NEARCTIC: Eastern North America.

Two females labeled "Georg." and "vittata, Alte Sammlung" were studied. One had a red Curran type label and is designated lectotype. The "Georg." locality label was probably added subsequently based on Macquart (1842:18).

Macquart (1842:18) identified this name as synonymous with *Psarus ornatus* Wiedemann and used *vittata* as the valid name. Previously Latreille (1825:495) described a new genus for an unnamed species from "Carolina," collected by Bosc and in the Paris museum. Macquart correctly associated all these descriptions. Despite the numerous citations to the contrary (i.e., Wirth et al., 1965:612), Macquart's designation of *vittata* is the first valid one for *Sphecomyia* (by subsequent monotypy and designation).

xanthaspis Wiedemann, 1830:191 (*Eristalis*). Type-locality: [none given]. Holotype female NMW. *Palpada distinguendus* (Wiedemann). NEOTROPICAL: Paraguay to Argentina.

Curran (1930:8) identified this name as synonymous with *Palpada distinguendus* (Wiedemann) based on examination of the types of both names. The female Curran studied was labeled as from "Buenos Aires" which lead Curran to suspect that it was not a type. From Wiedemann's description it is obvious that the lack of a locality for *xanthaspis* was merely an oversight or that he meant to cover it in his expression that *xanthaspis* was "*in jedem Betracht der vorigen . . . ähnlich*" (in every respect similar to the preceding (=*distinguendus*)). He did not formally describe *xanthaspis* as he indicated that it perhaps was the female of the preceding species (=*distinguendus*). Thus the description of *xanthaspis* does not include a Latin or German diagnosis nor length and locality statement. I studied the same specimen as Curran and have no doubt that it is the type of *xanthaspis* and the female of *distinguendus*.

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BIOGRAPHY AND BIBLIOGRAPHY

Petr Wolfgang Wygodzinsky (1916-1987)

BIOGRAPHY

Dr. Petr (Pedro, Peter, Wygo) W. Wygodzinsky died in Middletown, New York, on January 27, 1987 of complications from Parkinson's disease.

He was born in Bonn, Germany, on October 5, 1916 and educated at the University of Basle, Switzerland, where he received his doctorate in 1941 under the direction of Eduard Handschin. After a short time in Portugal, he emigrated to Brazil as a bicycle mechanic in 1941. However, through a woman he met aboard ship on the way to Brazil he was able to make contacts that allowed him to begin work as a taxonomist for the National Malarial Service within a short time of his arrival and later for the Ministry of Agriculture in Rio de Janeiro. During his stay in Brazil he became close friends with Herman Lent and Hugo de Souza Lopes.

In 1948 Wygodzinsky moved to Tucuman, Argentina, where he was employed as a specialist on the taxonomy of the Simuliidae at the Institute of Regional [Tropical] Medicine of the National University of Tucuman and where he was also Professor of Entomology and Genetics in the Faculty of Natural Sciences. He took this job in response to an advertisement for a simuliid specialist; although never having worked on the group, he assumed since he had mastered several other groups, black flies should present no particular problem. He moved to the Instituto Miguel Lillo, also in Tucuman, in 1954, where he pursued his taxonomic interests. From 1959 to 1962 Wygodzinsky served as Professor of Entomology at the National University in Buenos Aires, Argentina.

Wygodzinsky was a widely known and highly respected biologist in Argentina and Brazil. His legacy there includes disciples in entomology (Diptera, Heteroptera, and Coleoptera), botany, and genetics. In 1976 he was elected a Corresponding Member of the Brazilian Academy of Sciences. A year later, the University of La Plata recognized his contributions by conferring on him the title of Doctor Honoris Causa, an honor which was presented on the centenary of the Museum.

During his employment in Argentina he received two Guggenheim Fellowships (1955, 1960) to study at the University of California at Berkeley, with his close friend Robert L. Usinger. While at Berkeley he became acquainted with Jerome Rozen, then a graduate student at the University of California, who was much impressed with Wygodzinsky's entomological talents. After Rozen became chairman of the Department of Entomology at the American Museum, he offered a position to Peter, who accepted and moved to New York in 1962. Many times Wygodzinsky reflected on his indebtedness to Rozen for having made that opportunity possible. It was at the American Museum that he was able to pursue work on the large manuscripts that became one of his trademarks.

At the American Museum of Natural History, Peter was put in charge of the collections of Diptera and Heteroptera. The Museum had a large fly collection; he added mostly Simuliidae and Agromyzidae. The bug collection was modest, and dominated by members of the large and showy families. Wygodzinsky, bringing with him from South America a substantial collection of Reduviidae which was purchased

Fig. 1. Wygodzinsky (center) in the field; probably near Tafí del Valle, Argentina in the early 1950's. Two other men unidentified.

by the Museum, instituted a new period of growth in the bug collection. Through his efforts the Heteroptera collection of the Museum of Comparative Zoology was transferred to the American Museum as was a large collection of Dipsocoromorpha assembled by Michael Emsley. Wygodzinsky took particular pleasure in acquiring specimens of cryptic and ground dwelling Heteroptera and did much to build up those groups in the collections.

Peter was an exceptional and avid collector, securing specimens not only for his own work, but also for that of many others. He was acutely observant and extremely knowledgeable about where to catch insects. As a result, numerous species in many families and orders have been named for him from collections he made. He shunned mass collecting techniques because he wanted to see alive the creatures he was finding. He took much pride in discovering rarely found species.

In 1964 Peter married a young artist, Bona, then working at the Museum as a secretary in the Department of Entomology. She accompanied him on four collecting trips to Mexico and the Andean region of South America, where over a total of six months they collected and reared many species of black flies.

He had many successful field trips and preferred to work in higher latitudes and altitudes. He expressed his disinterest in the genus *Simulium* by noting that most

species, at least in South America, lived in the tropical lowlands. He collected in Argentina, Brazil, Chile, Peru, Ecuador, Colombia, Venezuela, Mexico, the Caribbean and North America. Peter recounted with a certain chagrin a black-fly-collecting trip to Peru and Chile in 1972. He and Sixto Coscarón arrived in Chile just before the military coup which overthrew Salvador Allende, and spent a good part of the time in their hotel watching the army take over the government and the country. One brief excursion to the countryside did yield a few important black flies. The next stop was Peru, in Cuzco Department and Machu Picchu. Unfortunately, there had been no rains and the local stream habitats had no water in them. Although he travelled widely in the New World he never returned to Europe and had no desire to do so. Though he valued the freedom of scientific enquiry that the Museum position allowed, he remained an Argentine citizen.

Wygodzinsky was the first scientist at the American Museum (and one of the first in North America) to introduce, employ, and argue for the efficacy of Hennig's methods of phylogenetics systematics. He believed this approach was the only one relevant for investigations in systematic biology and argued his point of view vigorously upon his arrival in New York in 1962. To him, those who could not see the importance of these ideas and employ them were simply "fuzzy thinkers."

Wygodzinsky thought it essential to make one's own illustrations in order to begin to understand the structure of the insect. Although he published about 21,000 illustrations, he often said he wanted to publish a monograph consisting entirely of illustrations. He was of the view that publishing productivity should be measured by a formula that included not only numbers of titles and pages, but also—and importantly—the number of illustrations made by the author.

He believed that compound microscopes and slide mounted specimens were essential to seeing and understanding the anatomy of insects. He routinely prepared illustrations while making microscopic observations, and thus began to amass basic manuscript materials. Many projects found their beginnings in the form of a few drawings of what he thought was an interesting specimen or structure. He believed in the adage that one picture is worth a thousand words, and had little patience with those who disparaged the value of illustrations.

Having gone to school in Europe and lived in South America, Wygodzinsky was fluent in German, English, Spanish, Portuguese and French. It was dazzling to watch him switch from one language to another when in the company of several people whose native languages were different. His use of English was remarkably versatile for an non-native speaker. He at times enjoyed mixing Portuguese and Spanish expressions with English for improved meaning or to convey a certain type of humor. Peter prepared a translation of Willi Hennig's paper "The Diptera fauna of New Zealand as a problem in systematics and zoogeography" (Wygodzinsky, 1966)—on his honeymoon!

Wygodzinsky had little taste for administrative duties, and on the one occasion at the American Museum when he served as the acting department chairman for a year and a half he found the task onerous and disheartening. Even the workday activities of the Museum seemed to be distracting at times, but what he might not have accomplished during the week he always more than made up for on the weekends. Although it was never particularly obvious from the outside, he was influential in the affairs of the American Museum and particularly the Department of Entomology.

Fig. 2.   Wygodzinsky at his microscope at the American Museum, about 1968.

Wygodzinsky's name was an anomaly to many, requiring such attention to spell that it was seldom spelled incorrectly. Peter knew he was the last of the Wygodzinskys, and a check by him of European phone books failed to turn up any listings of the name. His given name, on the other hand, changed from Petr to Pedro when he moved to South America and in North America some colleagues used "Peter." Most people ended up calling him Wygo or Pedro, but he responded gracefully to all.

Peter never drove an automobile, but in Argentina adopted the motorcycle as his preferred conveyance. Robert Usinger, in his autobiography (Usinger, 1972), commented that on a visit to Tucuman he would ride back and forth from his hotel to the Instituto Lillo on the back of Wygodzinsky's motorcycle. He used it to go on many field excursions in search of insects. Years later while walking the streets of New York he cast appreciative glances at motorcycles.

One of Peter's foremost loves was cats. He kept pictures, photographs, articles, books, and cartoons about them, and had two cats while in New York. He especially liked long-haired varieties. He often expressed the view that were he to have another life he would want to live it as a cat.

In the late 1970's Wygodzinsky realized that he had Parkinson's disease and began to put his affairs in order. He curated a large collection of Neotropical Agromyzidae and associated leaf mines that he assembled while in South America; this was a group that interested him much, but on which he never published. He also enlisted the talents of his Scientific Assistant, Kathleen Schmidt, to help finish a monograph of the genera of Western Hemisphere Enicocephalidae. This project was originally conceived as a joint effort with R. L. Usinger—Wygodzinsky to do the morphology and higher group work, Usinger to do the species treatments. Usinger's untimely death in 1968 terminated that plan, but Wygodzinsky never lost interest.

As a child Peter was interested in Lepidoptera, but they consumed so much storage space that he switched his attention to other groups, particularly the Heteroptera. His dissertation was a detailed morphological and life history study of the Diplura, Thysanura, and Microcoryphia of Switzerland (Wygodzinsky, 1941). He became acquainted with Herman Lent shortly after moving to Brazil and began to study the Reduviidae, often in collaboration with Lent. He also studied during this time the family Schizopteridae, producing the first detailed work on the morphology of the group.

Much of his time at Berkeley on Guggenheim Fellowships was devoted to a monograph of the assassin bug subfamily Emesinae, which, when finished in 1966, was one of the largest papers ever published by the American Museum and included more than 3,600 figures. His final major paper on the Reduviidae was a revision of the Triatominae co-authored with Herman Lent and published by the American Museum of Natural History (1979). He continued studying the black fly fauna of the Andean region, mostly in cooperation with Sixto Coscarón of La Plata, Argentina, which work was supported in part with research funds from the National Science Foundation. Of the several important papers published on the group, probably the most significant will be the forthcoming "Revision of *Gigantodax*," co-authored with Sixto Coscarón, with its discussion of the classification of the genus based on descriptions of larvae, pupae, and adults of 64 species, 36 of them new.

During his career, Wygodzinsky published in excess of 250 scientific papers (see Bibliography). His work will stand not only for it prodigious and detailed nature, but also for its breadth of coverage, something accomplished by few systematists in this day and age.

Though a private individual, Peter was a warm and gentle person who was much concerned about and interested in the problems, affairs, and triumphs of his friends and colleagues. Each morning, without fail, he visited every member of the Department to chat for a while. He was loved by all and it was with much pain and sadness

that we watched his gradual deterioration and debilitation brought on by Parkinson's disease. Even years later we still remember, think, and talk about Wygo; he was an affecting man.—*Randall T. Schuh and Lee H. Herman, Department of Entomology, American Museum of Natural History, New York, New York 10024.*

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BOOK REVIEWS

Immature Insects.—Frederick W. Stehr (ed.). 1985. Kendall/Hunt Publishing Company, Dubuque, Iowa. xiii + 754 pp. No price supplied.

This impressive volume is a direct outgrowth of Alvah Peterson's *Larvae of Insects,* Parts I and II (1956 and 1957). Authored by 45 contributors, the work was organized and coordinated by Frederick W. Stehr who also wrote a number of the included chapters. The dedication acknowledges Peterson's influence on Stehr, and the stated purpose and organization strongly reflect Peterson's two earlier works. The scope of this and the soon-to-appear second volume differs from the earlier versions in that Peterson treated the immatures of only the Holometabola; Stehr's volumes will cover all of the Insecta.

Immature Insects is designed to provide a means to identify the immature stages of insects to the family level for North American taxa and to give the reader information about where to find more detailed accounts of their classification, morphology, life histories, and ecologies. The preface points out that the work "has been designed to serve as: (1) a textbook for courses on immature insects; (2) an introduction to and partial source for literature on immature insects; (3) a means of identifying the larvae of all orders to family; (4) a means to identify a number of common economically important or unusual species (largely North American) using the abundant illustrations, descriptions and/or selected keys; and (5) a source of information on the biology and ecology of the families of selected important species. The emphasis is on larvae, with minimal coverage of eggs and pupae, since knowledge of the latter is *relatively* meager and the need to identify them is not great compared with larvae and adults."

Chapter 1 introduces the reader to definitions of important terms pertaining to immature insects and to their metamorphosis. Chapter 2 provides a handy reference on how to collect and rear immature insects, methods on killing, fixation and preservation (including formulae for killing, fixing and preserving fluids) and how to label, store, mount, illustrate and ship specimens. Chapter 3 enters the heart of the volume by offering a key to the orders of immature insects and selected arthropods. This key (as well as all others in subsequent chapters) is carefully presented, fully illustrated and allows the reader to identify mites, scorpions, ricinuleids, whip scorpions, sun spiders, pseudoscorpions, phalangids, crustacea, chilopods, diplopods and symphylans, in addition to the orders of insects. Chapter 4 begins the treatment of the first order, the Protura (here regarded a separate class). Chapters 5 and 6 are on the class/order Collembola and the class/order Diplura respectively. Chapters 7 through 27 present information about each of the following: Microcoryphia, Thysanura, Ephemeroptera, Odonata, Blattodea, Isoptera, Mantodea, Grylloblattodea, Phasmatodea, Orthoptera, Dermaptera, Embiidina, Zoraptera, Plecoptera, Psocoptera, Mallophaga, Anoplura, Mecoptera, Trichoptera, Lepidoptera, and Hymenoptera. (The next volume will cover the remaining hexapod orders.) Not too surprisingly, more than half of the book is devoted to the last two orders, and Lepidoptera receives by far the greatest attention. Treatment of each order is similar but not identical. Normally an order is briefly discussed in an introductory section, the biology and ecology of the group is presented, a diagnosis follows, (whereby immatures of the

order can be distinguished from those of other orders), and then the anatomy of the immatures is explained. In some chapters specialized techniques for finding, collecting, and preserving are also given. Each chapter then delves into the classification of the order and presents a key to the families followed by individual descriptions of the families. The chapters are fully illustrated, and the subsections of a chapter have synoptic bibliographies referring the reader to the usually extensive terminal chapter bibliography. At the end of the volume there is a single glossary of the common terms used in descriptions of immature insects and a host-plant and substrate index.

This first volume of the series is indeed a monumental reference work (far more complete than a textbook) for there never has been such a complete exposition treating immature insects. Contributors are among the leading specialists in their particular groups, accounting for the work's high degree of authority. Stehr is to be congratulated for imposing reasonable consistency of format, no easy task considering the number of contributors. Illustrations range from very good to excellent on my score card. Remarkable is the fact that the illustrations are labelled with complete terms rather than abbreviations, a practice in biology that should have (but did not) become extinct at the end of the Cretaceous. The text is written in a straightforward explanatory way and presents a wealth of information pertaining to the biology, anatomy and classification of immatures.

How might the volume have been improved? The answer is perhaps "in no way," considering its high level of scholarship and the constraints imposed by the size of the Insecta. But several points might be worthy of consideration for the next generation of works on immatures. First, although not restricted to this continent, the focus of the current volume is North America. Systematists almost certainly would like to see coverage increased to worldwide, particularly with respect to significant taxonomic elements that do not occur in North America. If such an approach were planned, resulting publication would probably have to be by order rather than class because of the size of the task. Second, although the expressed purpose of the volume is to enable identification of immatures, something might be (and I think should have been) said about using immatures in determining evolutionary relationships of taxa. Immature insects are not merely something to be identified, but are sources of information that shed light upon the phylogenies of taxa. To an extent this is implied in the write-ups for individual families and orders, but a student relying on the book would not come away imbued with the fact that immatures are a storehouse of information rife for phylogenetic interpretation or with a strong feeling that interordinal relationships can be evaluated using immatures.

These points aside, this volume and presumably the following one will be lasting compendia of information about immatures and about how to find out more about them; they are unique reference works, direct descendents of Alvah Peterson's *Larvae of Insects*. We can safely say that Pete would have been proud of the next generation of his pioneering work.—*Jerome G. Rozen, Jr., Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024-5192.*

<div align="center">LITERATURE CITED</div>

Peterson, A. 1956. Larvae of Insects, an Introduction to Nearctic Species. Part I. Lepidoptera and Plant Infesting Hymenoptera. Edward Brothers, Inc., 315 pp.

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The Butterflies of Costa Rica and Their Natural History. Papilionidae, Pieridae, Nymphalidae.—Philip J. DeVries. 1987. Princeton University Press. 327 pp. Prices: $60.00 cloth; $22.50 paper.

Phil DeVries has written an extremely important work, possibly the best field guide available for any group of Neotropical organisms. It sets a new standard for butterfly guides. The first chapter discusses biology and systematics of butterflies. Included are some rather unusual speculations concerning wing pattern development and mimicry. In chapter two, the major faunal regions and butterfly diversity of Costa Rica are described. The following chapters constitute a field guide to Costa Rica's butterflies, broken down by family. Diagnoses are given for each family, subfamily, genus and species. Included in the field guide section are over 50 pages of color plates showing dorsal and ventral views of adult butterflies, and close to 20 pages of line drawings showing immature stages.

The book derives its strength from several things: First, the color photographs of adult butterflies and line drawings of immatures are superb. Since field identification is the book's main function, the color plates alone make it a success. I lack the knowledge to evaluate whether each taxon DeVries treats is accurately named and identified, but since he spent much time studying the butterfly collection at the British Museum and consulting with the experts there, one can have considerable confidence that they are. Secondly, DeVries provides all the available distributional, habitat, and life history data for Costa Rican butterflies. The quality and quantity of this information will make those interested in other Neotropical insect groups envious. Many of the hostplant records and life histories were collected by DeVries himself, and are listed in an earlier paper (DeVries, 1985). A tremendous amount of field knowledge has obviously gone into this guide. DeVries seems to have an understanding and appreciation for the land of Costa Rica that can only come from time and effort. Thirdly, although DeVries did not intend to provide a complete literature for the taxonomy and biology of Costa Rican butterflies, the bibliography is well selected and extremely comprehensive. It will provide a useful reference for people interested in all aspects of butterfly biology. In conclusion, I can only say that DeVries' book is a must-to-have for any student of the Neotropics.

As a reviewer, I hate to heap too much praise on someone's work. It's just not good policy. Here are my criticisms:

The chapter on general biology, morphology, and systematics of butterflies is written for a beginning amateur, and is probably too basic for most of those who will buy the book. The quality of treatment for these subjects is not lower than that found in other field guides, but it is not very good in any of them. The section as a whole could have been greatly shortened without much loss of important information.

Within the sections on each family, characters that DeVries lists to define groups are usually plesiomorphic, rather than being traits unique to a particular group. For example, the Papilionidae are "distinguished by six walking legs that bear nonbifid

claws; forelegs that bear an epiphysis;" (p. 61), and on it goes. These traits are also handy for distinguishing Lepidoptera from caddisflies, or insects from monkeys. Such is the field guide approach; it is adequate when identification is the sole aim.

One of the book's most important features is the detailed distributional and habitat data, but the two maps provided are not of high enough quality to make the most of this information. In addition to these general maps, I would like to have seen a series of high quality, detailed maps included, showing topography, vegetation types, etc.

DeVries adopts what I consider to be intelligent butterfly classifications. For example, *Papilio* is retained as a single genus, and Nymphalidae is recognized in the broad sense. However, there are indications in the book that DeVries' rapport with the systematic community could use improvement. He is troubled by the "strong component of emotionalism or even fanaticism in the "war" among various factions" (p. 32) of systematists, referring here to the evolutionary, phenetic, and cladistic "factions." It sounds sort of frightening, doesn't it? Something akin to the Persian Gulf. I take issue with his statement, being of the opinion that this "jihad" has produced some of the most significant advances in comparative biology since, oh say, the advent of the pencil. But of course I happen to belong to one of these terrorist cells, and am therefore seeing the picture through crazed eyes.—*James S. Miller, Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024.*

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The Lives of Butterflies.—Matthew M. Douglas. 1986. University of Michigan Press, 241 pp. $45.00.

The study of butterflies has made important contributions to the development of systematics, evolutionary biology, and ecology. Using mainly temperate American examples this book selectively summarizes the biology of butterflies with the aim of providing professional biologists and graduate students a literature base for further research.

After an introduction to contemporary theories about the evolution of insect wings, the formal text begins with a treatment of the phylogenetic origins of the butterflies. Douglas then proceeds to discuss the morphology and physiology of both early stages and adult butterflies, and then covers topics relevant to behavior, population and community ecology, and population genetics. The book concludes with a chapter on coevolution of butterflies and plants, and a postscript encouraging future research. Throughout the text Douglas admirably maintains a strong evolutionary perspective. Two appendices are included that illustrate the geologic time scale and present a list of some butterfly species used in research (both appendices could be deleted without loss to content). The bibliography contains many solid references essential to doing

butterfly research. The illustrations in the first few chapters (but none in the last chapters) and a small section of good color photographs make this book pleasing to the eye. The price, however, is apt to make potential buyers think twice and restrict the book's circulation.

The text is written in an engaging and enthusiastic style that generally gets to the point quickly, covers the subject at a good pace, and contains a minimum of misspellings. Some careful gardening could have condensed the book and eliminated a lot of repetious phrasing, especially the sections on population biology, migrations, and genetics, which tend to wander around. These criticisms aside, overall Douglas provides us with a good summary for some aspects of butterfly biology and encourages experimental biology as a productive method of furthering research in the field. In this regard the author's own hypotheses and leading questions sprinkled throughout should provide food for thought to some biologists actually doing research on butterflies. The balanced treatment of functional morphology, physiology, organismal, and molecular studies makes this book a useful tool for students of butterflies and to those with a general interest in organismal biology.

For our tastes the book is rather thin on the broad natural history patterns and the ecology of tropical and European butterflies—major sources of information and potential experimental material. Very puzzling is that it is completely unblemished by the notion that systematics is a predictive and necessary tool in butterfly research. We think the author will agree that the majority of researchers take advantage of phylogenetic patterns. Ultraviolet reflectance patterns, osmeteria, sinigrins as feeding stimulants, adult feeding behaviors, genetic polymorphisms, mutualisms with ants, mimicry, and coevolution are not characters that occur randomly or equally among all butterfly groups.

The erratic flight paths and aerodynamically curious wing shapes of butterflies have always attracted considerable attention. Douglas presents, perhaps for the first time in the secondary literature, an introductory discussion of the thoracic musculature, wing shape, and aerodynamics of flight in butterflies. This is an exciting area of research, and as such merits in a book of this character further treatment, even if only greater citation of the primary literature. Perhaps inevitably when dealing with the complicated subject of aerodynamics, a number of erroneous statements are bound to arise. For example, lift on an aerofoil below the stalling point does not decrease but rather increases with increasing angle of attack (p. 51). The notion that butterfly scales enhance aerodynamic performance of the wings (p. 55) is widespread, but is based on the results of only one disputed study (see Martin & Carpenter *In:* W. Nachtigall (ed.) 1977, *Physiology of Movements, Biomechanics*, Gustav Fischer, Stuttgart). Douglas suggests that even stereotypical "knock-kneed lepidopterists" can catch the fastest butterflies, but as experience in the field will tell, the reason butterflies are in general difficult to catch in free flight relates not to their speed of flight but rather the unpredictable character of the flight path and their extraordinary capacities for maneuverability.

Chapter 8 shows a great enthusiasm for coevolution as a unifying theory in community ecology and evolution and Douglas should be applauded for his efforts. However, some examples used to illustrate coevolution are slightly misleading or simply wrong: Lycaenids and ants are very clearly **not** co-evolved (p. 178)—removing all the lycaenids in the world would have little effect on ants. Butterflies are typically

not plant predators (p. 187)—butterflies typically remove small fractions of their hostplant biomass and do not kill them. It is doubtful that *Heliconius* adults sequester alkaloids from coevolved larval feeding on *Passiflora* (p. 190)—their distasteful properties are derived from the ability to feed on pollen as adults.

The value of over 350 references to diverse and important research papers in the bibliography will not be lost on students of butterflies. However, including other references besides Gilbert and Shapiro from Vane-Wright, R. I. & P. Ackery's, (eds.), 1984, *The Biology of Butterflies*, Symp. Roy. Ent. Soc. 11, and crediting authors of primary research (not just the review author), would further increase the book's utility as a research sourcebook. We feel a citation to certain facts alluded to by Douglas would have been appropriate and led us to the reference (e.g., Flight muscle mechanism and wing articulation, p. 49; 100 hostplants for the painted lady, p. 115; mites reported to weaken butterflies, p. 137; shared flavinoids between Polygonaceae and Rosaceae, p. 179).

In summary, this is a valuable introduction to the field of butterfly biology, and ranks as one of the first contemporary presentations of the wide range of biological investigation on the butterflies. As such, it must not be expected to be the balanced, comprehensive presentation of the field, as was Ford's *Butterflies* in its day. We eagerly anticipate future contributions to the genre which integrate natural history, systematics, and the evolutionary ecology of butterflies from all regions. *The Lives of Butterflies* would be an appropriate companion to such works.—*P. J. DeVries and R. Dudley, Smithsonian Tropical Research Inst., Box 2072, Balboa, Panama.*

A Scanning Electron Microscope Atlas of the Honey Bee.—E. H. Erickson, Jr., S. D. Carlson, and M. B. Garment. 1986. Iowa State University Press, Ames, Iowa. 292 pp. $51.95.

Poring over an atlas, whether geographical or anatomical, should stimulate the imagination and the sense of adventure. Large pages, multiple illustrations of unknown territories, an abundance of factual detail and varying textures—this is the stuff that feeds the urge to explore. I am pleased to report that this book is a success in these respects. The hundreds of micrographs and photomontages illustrating the surface structures of worker, queen, and drone honey bees, carefully chosen and tastefully arranged on expansive 9 × 12 pages, are at once a dazzling display of present knowledge and an invitation to plunge into the many morphological mysteries that remain unresolved. For although we have more knowledge of the biology—behavior, physiology, morphology—of the honey bee than of any other insect (and indeed almost any other animal species), the figure captions crackle with phrases such as "function unknown," "maybe," and "seems to be." The call to further exploration is clear.

Unfortunately, the high technical and esthetic standards met by the micrographs were not uniformly applied to the rest of this book. The line drawings of the Appendix, although helpful and adequate, are sadly lacking in the beauty and charm of R. E. Snodgrass' classic illustrations in *The Anatomy of the Honey Bee*. The fairly short

text passages contain several errors. A few examples: the annual monetary values of the U.S. beekeeping industry and of bee-pollinated agricultural crops in the U.S. are misstated (appropriate estimates would be about $100 million and $10–20 billion, respectively); beeswax does not serve a useful function in the production of honey beer; and there is no evidence that feral honey bee swarms choosing home sites prefer living trees to dead ones. Especially disappointing is the inclusion in the text of such statements as "the drone's sole purpose for being is mating" and "[the queen's] only complex behavior seems to be that of seeking out and killing sister queens and mating"; these canards, which occur frequently in the popular biological literature, are expressions of poor biological thinking. A final criticism is that many of the statistics are given without regard for the appropriate number of significant digits. Thus, for instance, in the presentation of the fascinating fact that after 500 miles of accumulated distance flown the body of a worker honey bee physically breaks down, the figure is converted to the impossibly precise 804 km.

However, to return to the bright side, this book does have an extensive glossary, the index has been well put together, and the plate layouts have style and grace. This atlas should excite students and researchers about the possibilities of further investigating honey bee biology and, indeed, all aspects of invertebrate morphology.—*Richard Nowogrodzki, Department of Entomology, Cornell University, Ithaca, New York 14853.*

The Behavioural Ecology of Ants.—John H. Sudd and Nigel R. Franks. 1987. Chapman & Hall and Methuen, New York. x + 206 pp. Price: $55.00 cloth; $23.00 paper.

There are approximately 1,200 living species of ants, and the variation and complexity of their social organization is unique in the animal world. Ant colonies are characterized as *eusocial,* because they have overlapping adult generations, cooperative brood care, and sterile worker castes. According to the authors, this small volume primarily concerns two related issues: (1) how eusociality has evolved under the influence of natural selection; and (2) why it is found only in termites, ants, and some species of bees and wasps. Although, the authors succeed in their mission, it is somewhat misleading. For in addition to providing a theoretical discussion on the evolution of social behavior in insects, the book provides an excellent up-date on the behavior and ecology of a wide variety of ant species.

After an introductory chapter on kin selection and its influence on the number of queens in ant colonies, the authors provide a brief review (Chapter 2) of ant phylogeny. This is not so much a systematic treatment as it is a discussion of the major ecological and behavioral differences among the approximately 12 ant subfamilies.

Chapters 3 and 4 are a bit more esoteric, dealing with "economics" and caste structure. The former topic considers issues such as the time-course of colony growth and reproduction, while the latter focuses on division of labor among individuals differing in morphology or age. Age-related jobs are called temporal polyethism, the best example being that young individuals typically stay in the nest and tend the brood, while foragers are almost always the oldest workers.

The next three chapters include a heavy (and refreshing) dose of ant natural history. Thus Chapter 5 reviews the recent literature on the mechanisms of communication among ants, including the pheromonal basis for nest recognition, alarm behavior, recruitment to food, and mating. Chapters 6 and 7 are complementary, and consider how communicatory processes are used by ants to interact with other organisms. These topics range from ant-plant associations on the one hand, to parasitic relationships that ants have with closely related species. The section on slave-making behavior is particularly noteworthy for its inclusion of some very recent research on the ontogeny and evolution of social parasitism.

This small volume doesn't pretend to include every aspect of ant ecology and behavior, but what is does cover, it covers well. Perhaps my biggest complaint is with the all too frequent use of anthropomorphic ecological metaphors. For example, just about everything the ants do for a living is called a "strategy." The term "strategy" has clearly become the ecologist's equivalent of the ethologist's concept of "instinct." It is a vacuous term which is applied to everything, but which explains nothing. My second-place vote goes to the term "resource." And exactly what is a resource? Not simply food, water, or nesting material. According to Sudd and Franks, even information is a (non-tangible) resource. Thus the beginning student is left with the notion that ants (as well as every other living organism) have evolved a wide variety of strategies to conserve resources. Profound, it's not!

Finally, the cover of the book proclaims that *The Behavioural Ecology Of Ants* is a "Tertiary Level Biology" text. Translation: it is written for advanced undergraduates, postgraduates, and researchers in entomology, ecology, and animal behavior. But thanks to the lucid treatment by the authors, most of this book is not technical, and will be of interest to anyone fascinated by the diversity of social organization in the ant world. — *Howard Topoff, Department of Psychology, Hunter College of CUNY, New York, New York 10021.*

Announcement: A special field course on insects of the Maine coast will be taught from June 26–July 2 at Eagle Hill Wildlife Research Station, located 35 miles east of Bar Harbor. The course will be taught by Richard Dearborn, senior entomologist of the State of Maine. The course is on a research participation basis (tax deductible). The station is beautifully located on a 235 foot high hill at the edge of the ocean. For more information about this and other courses write or call: Eagle Hill Wildlife Research Station, Dyer Bay Road, Steuben, Maine 04680. 207-546-2821.

INSTRUCTIONS TO AUTHORS

The *Journal of the New York Entomological Society* is devoted to the advancement and dissemination of knowledge of insects and related taxa. The costs of publishing the Journal are paid by subscriptions, membership dues, page charges, and the proceeds from an endowment established with bequests from the late C. P. Alexander and Patricia Vaurie. The Journal will consider for publication manuscripts of any length dealing with original research in entomology. Longer papers will be printed as articles, shorter ones as "scientific notes." Book reviews will be solicited by the Book Review Editor.

Manuscripts should be submitted in duplicate to: Dr. Randall T. Schuh, Editor, Journal of the New York Entomological Society, c/o Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024. All material must be double-spaced (including references, tables, captions, etc.) and prepared in the format of a recent issue of the Journal.

Longer manuscripts intended for submission as articles should be accompanied by a brief abstract. Footnotes should be avoided. Tables should be prepared as separate pages; they should be kept to a minimum because of the high cost of typesetting, but may be submitted as photographically reproducible material (see below). The list of references is headed "Literature Cited" and should follow the format indicated in the CBE Style Manual or as found in a recent issue of the Journal.

Illustrations (originals whenever possible) should be submitted flat, never rolled or folded, with the manuscript. Size of illustrations should be kept manageable and suitable for shipment through the US mail without being damaged. Proportions of illustrations should conform to single column format, actual page size 11.5 × 17.5 cm. Please assemble illustrations in a compact fashion in order to use journal space effectively. *Mount line drawings and halftones on separate plates.* Figures should be numbered consecutively. Figure captions should be double-spaced, grouped together and placed at the end of the manuscript. If tables are submitted for photographic reproduction, they should be neat and clean and conform to journal format proportions.

Authors will receive page proofs, with the original manuscripts, directly from the printer. Corrected proofs should be returned promptly to the Editor to avoid publication delays. Revisions in proof should be kept to the absolute minimum. *Excessive alterations in proof will be charged to the author at the rate of $2.00 per revision line.*

Society members will be charged a fee of $20.00 per printed page and $5.00 per plate of figures. Non-members will be charged $45.00 per printed page and $5.00 per plate of figures. Member authors who do not have institutional funds may petition to the Society for waiver of page charges for no more than eight pages on a once a year basis. Because of limited funds, all such requests will be handled on a first-come first-serve basis.

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Journal of the
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Meetings of the Society are held on the third Tuesday of each month (except June through September) at 8 p.m. in the American Museum of Natural History, Central Park West at 79th Street, New York, New York.

Mailed August 12, 1988

ZOROTYPUS PALAEUS, NEW SPECIES, A FOSSIL ZORAPTERA (INSECTA) IN DOMINICAN AMBER

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Abstract.—The first fossil member of the order Zoraptera (Insecta), *Zorotypus palaeus,* new species is described from amber originating from the Dominican Republic. The description is based on a single, apterous, chitinized female lacking eyes and ocelli. The amber came from mines located in the Cordillera Septentrional in the Altamira facies of the El Mamey formation. Sedimentary and geological evidence indicate a range of lower Miocene to upper Eocene for the amber from this region.

A piece of amber from the Dominican Republic was observed to contain a member of the order Zoraptera. The piece had been purchased by J. Brodzinsky in 1985 and Dr. José Mari-Mutt (Puerto Rico) was the first to recognize one of the entrapped insects as a member of the Order Zoraptera. This piece was included in the Brodzinsky-Lopez-Penha collection later purchased by the Smithsonian Institution.

The Zoraptera constitute the smallest order of insects and represent a single family, the Zorotypidae, with a single genus *Zorotypus,* represented by 28 described species. The present find represents the first fossil representative of this order. The amber piece came from mines located in the Cordillera Septentrional in the Altamira facies of the El Mamey formation, a shale-sandstone interspersed with a conglomerate of well rounded pebbles which has been assigned to the upper Eocene (Eberle et al., 1980). Prior dating of amber from the Palo Alto mine in the Cordillera Septentrional based on an analysis of foraminifera counts suggested a lower Miocene age (Baroni-Urbani and Saunders, 1980). Thus, sedimentary and geological evidence indicate a range of lower Miocene to upper Eocene for the amber mines in the Cordillera Septentrional.

MATERIALS AND METHODS

The amber piece containing the apterous female zorapteran weighed 1.8 grams and was triangular-shaped in outline, measuring 17 mm × 17 mm × 18 mm, with a thickness of 8.5 mm. The piece also contained three complete adult Formicidae, 3 complete adult Staphylinidae and 2 complete Dermaptera.

The specimen was observed under both dissecting and compound microscopes at magnifications of 20 to 200×. Drawings were made with the assistance of a camera lucida.

RESULTS

Comparison of the fossil specimen with descriptions of recent species indicated that it is new to science and a description follows below.

Zoraptera Silvestri 1913
Zorotypidae Silvestri 1913
Zorotypus Silvestri 1913
Zorotypus paleus, new species
Figs. 1–7

Description. APTEROUS FEMALE: The specimen is well preserved although a portion of the middle right leg is missing as are some portions of the dorsal plates on the head (Fig. 1). Body length without antennae, 2.9 mm; length of antenna 1.6 mm; mouthparts, mandibulate; maxillary palp 5-segmented, labial palp 3-segmented; right antenna 8-segmented, left antenna 9-segmented; all tarsi 2-segmented; cercus 1-segmented; wings, compound eyes, ocelli and fontanelle absent; all sclerites and appendages dark-pigmented; abdomen with 10 segments; cerci present; gonopore just posterior to the seventh sternite (hypogynium), which is emarginate medially (Fig. 2); the apex of a sclerotized, trough-shaped structure (possibly representing the ovipositor) issues from the gonopore; eight abdominal sternite narrow, yet complete, partially overlaps segment nine which is non-sclerotized and composed of a short, medial, emarginate section and an apically narrowed central portion forked at the apex (possibly representing styli); sternite ten sclerotized on opposing lateral posterior surfaces beneath cerci; the sclerotized surfaces could be paraprocts; tergites eight, nine and ten abdominal are complete (Fig. 3); tergite nine with posterior medial margin extended, tergite ten posterially emarginate; cerci distinct, each with 4 large and 1 small setae; sclerotized patches on dorsal anterior and posterior bases of cerci (Fig. 3); thoracic tergites typical sclerotized, with a series of setae; antennal segment one longest, followed by the smallest (second) and next-to-smallest (third) (Figs. 4, 7); flagellomeres four–eight on right side and four–nine on left side elongate and subequal in length and width; right antenna with only eight flagellomeres, but fifth to eighth segments are proportionally longer than segments four to nine on left antenna; thus both antennae are approximately equal in length. Left hind femur with three long setae and a spine on outer apical margin, and a long seta flanked by two smaller ones on outer posterior margin (Fig. 5); inner femoral margin well developed with a row of four spines and two apical setae; three spines occur on inner margin of the hind tibia; outer margin of hind tibia with long seta between basal and subbasal spines; basitarsus small without setae; second tarsal segment with rows of short setae; claws paired, equal, typical for the genus (Figs. 5,6).

Holotype. Apterous female; in piece #7406 of the Brodzinsky-Lopez-Penha amber collection in the Department of Entomology of the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Source. Mines from the Cordillera Septentrional in the Dominican Republic. Exact locality unknown.

Discussion. Some interesting aspects of zorapteran morphology have been acquired from this investigation. Both Gurney (1974) and Riegel (1987) have described two types of individuals in their resumés of the order Zoraptera. One of these is a pale apterous form which has the eyes rudimentary or absent; the other is a winged, dark-pigmented type with compound eyes and ocelli. The fossil form represents an intermediate stage lacking eyes but being dark-pigmented. This type was recognized by Caudell (1920) as "an apterous form, fully chitinized and superficially resembling

Fig. 1.   *Zorotypus palaeus* holotype in Dominican amber.

the dealated chitinized adult of *Z. hubbardi* but differing in having neither eyes nor ocelli." Gurney (1938) considered this observation as a misunderstanding, however the present study indicates that Caudell (1920) was indeed correct in establishing a third morphological type for the Zoraptera.

Adult Zoraptera are known to possess nine-segmented antennae whereas the nymphs normally have eight-segmented antennae. Since the fossil specimen possesses one eight- and one nine-segmented antenna, but on the basis of the gonopore and terminal abdominal segments is an adult, the thought arose that the ninth left antennal segment had been broken off. However Caudell (1920) reported a similar condition in an "apterous unchitinized adult" of *Z. hubbardi*. He stated "one specimen has one antenna normal while the other one is abnormal in having but eight segments instead of nine; that this abnormal antennae is complete is shown by the structure of the terminal segment." Thus, the fossil condition of the antennae is considered natural although abnormal.
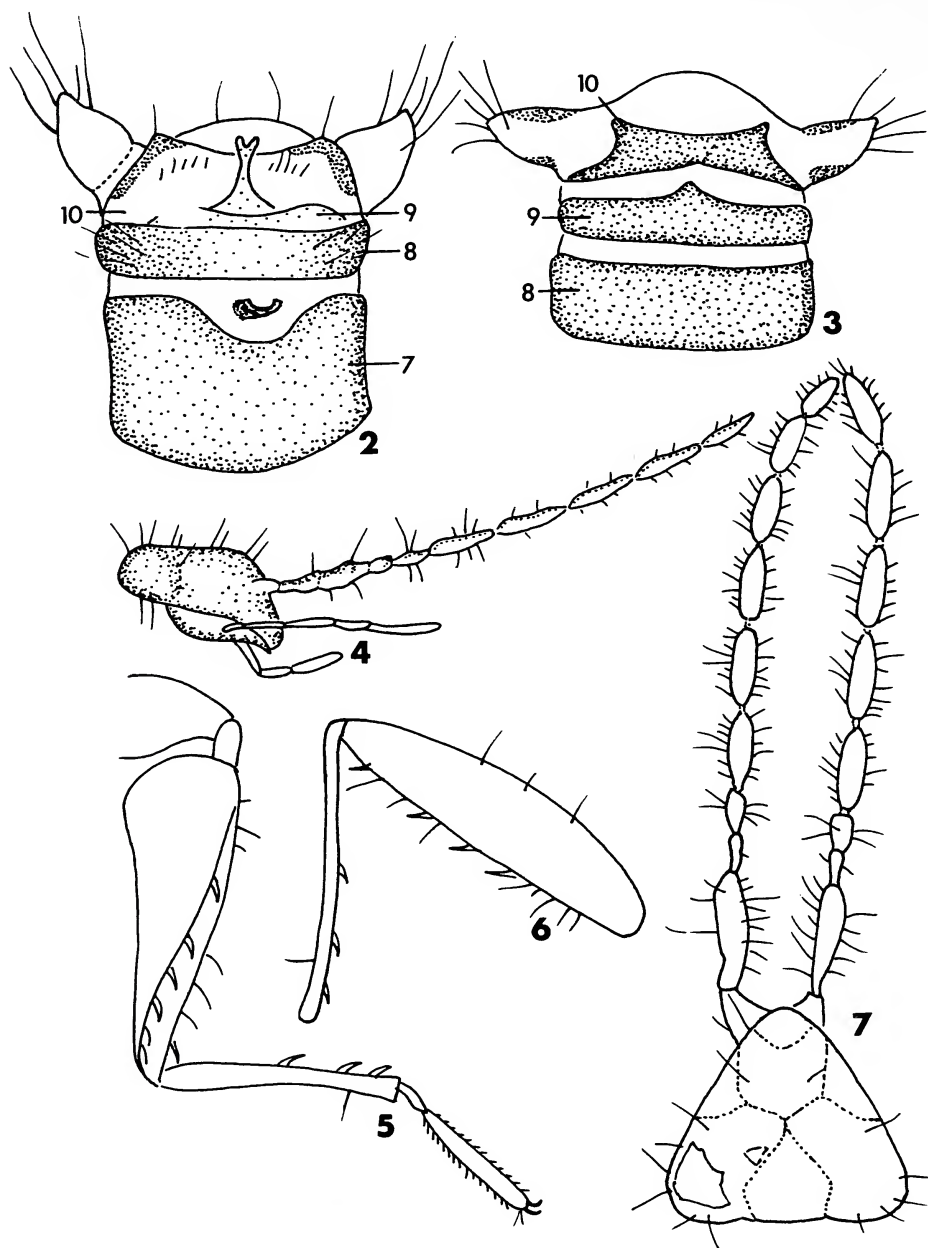
Figs. 2–7. *Zorotypus palaeus.* 2. Terminal abdominal sternites. 3. Terminal abdominal tergites. 4. Lateral view of head, showing labial and maxillary palpi and right antenna. 5. Left hind leg. 6. Right hind leg. 7. Dorsal view of head and antennae.

Table 1. Chronological list of published species of *Zorotypus* with known distribution.

Species		Distribution
Z. javanicus Silvestri	1913	Indonesia
Z. ceylonicus Silvestri	1913	Ceylon
Z. guineensis Silvestri	1913	Guinea
Z. neotropicus Silvestri	1916	Costa Rica
Z. hubbardi Caudell	1918	North America
Z. snyderi Caudell	1920	Jamaica, North America
Z. swezeyi Caudell	1922	Hawaii
Z. manni Caudell	1923	Bolivia
Z. silvestri Karny	1926	Indonesia
Z. caudelli Karny	1926	Sumatra
Z. longicercatus Caudell	1927	Jamaica
Z. buxtoni Karny	1932	Samoa
Z. zimmermani Gurney	1938	Fiji
Z. cramptoni Gurney	1938	Guatemala
Z. barberi Gurney	1938	Cocos Island
Z. philippinensis Gurney	1938	Philippines
Z. shannoni Gurney	1938	Brazil
Z. mexicanus Bolivar Pieltain	1940	Mexico
Z. brasiliensis Silvestri	1946	Brazil
Z. delamarei Paulian	1949	Madagascar
Z. vinsoni Paulian	1951	Mauritius
Z. huxleyi Bolivar Pieltain and Coronado-G.	1962	Peru, Brazil
Z. congensis Van Ryn-Tournel	1971	Congo
Z. sinensis Hwang	1974	China (Tibet)
Z. medoensis Hwang	1976	China (Tibet)
Z. lelupi Weidner	1976	Galapagos
Z. weidneri New	1978	Brazil
Z. hamiltoni New	1978	Colombia

There are at present 28 described species of *Zorotypus* (Table 1), mostly from the New and Old World tropics, however *Z. hubbardi* is unusual in extending its range into the North American temperate zone, although this may be dependent on it locating microclimates which simulate sub-tropical conditions. Specimens of *Zorotypus* have been collected from the Dominican Republic by E. Ross. These have been identified as *Z. barberi* by Jae Choe at the Museum of Comparative Zoology, Harvard.

On the basis of the size and shape of the antennal segments, cerci, tibia and tarsal segments, terminal abdominal tergites and sternites as well as the setal and spinal armature of the hind femora and other parts of the body, the fossil specimen can be separated from all the species listed in Table 1. It should be noted that the fossil specimen is a female and that in comparison with species described only from males, it is assumed that the cerci and antennal structure are similar in both sexes. This has proven to be the case, but unfortunately does not hold true for the armature on the hind femur, which tends to be more strongly developed in males.

Aside from representing the first record and description of a fossil zorapteran the

present report is apparently the first time that the position of the female gonopore has been definitely established for the order. It is interesting to note that the location of the gonopore and the structure of the seventh sternum is very similar to the condition found in female termites. Also the presence of what appears to be the tip of a sclerotized ovipositor is interesting since among the Isoptera this structure is known to occur only in a few species of lower termites (Roonwal, 1970).

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NEOMEGAMELANUS ELONGATUS (HOMOPTERA: DELPHACIDAE): DESCRIPTIONS OF IMMATURES

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Abstract.—Eggs and first through fifth instar nymphs of *Neomegamelanus elongatus* (Ball) are described and illustrated. Features useful in separating nymphal instars include differences in body size and proportions, spination of metatibiae, metatibial spurs, metatarsomeres, and number of metatarsomeres and body pits.

The genus *Neomegamelanus* was erected by McDermott (1952) for five species of small, slender planthoppers with cone-shaped heads. Four of the species are apparently restricted to coastal plain habitats and range from Massachusetts south to Florida and west to Texas and Mexico (McDermott, 1952; Wilson, pers. obs.). The fifth species, *N. spartini* (Osborn), is recorded from Maine to Florida and Mississippi (Metcalf, 1943) as well as Ohio (Crawford, 1914). This only inland record is quite likely in error as Osborn (1905) recorded *Spartina patens* (Ait.) Muhl., a plant generally restricted to coastal salt marshes (Mobberley, 1956), as the host plant of this species.

Little information is available on the biology of any species of *Neomegamelanus*. *N. dorsalis* (Metcalf) is trivoltine in New Jersey, overwinters as nymphs, feeds on salt meadow cordgrass, *S. patens* (Denno, 1977, 1978, 1980), and has been reported to occur on salt grass, *Distichlis spicata* (L.) Greene (Tallamy and Denno, 1979). *N. elongatus* (Ball) has been collected by sweeping *S. patens* (Denno, 1978). *N. spartini* (Osborn) was collected from flowering heads of *S. patens* (Osborn, 1905). *N. penilautus* McDermott has been swept from *S. spartinae* (Denno, 1978). *N. lautus* (Metcalf) was reported to occur in the "Spartina association" (Dozier, 1926).

This paper presents descriptions and illustrations of the egg and first through fifth instars of *N. elongatus*.

DESCRIPTIONS

Specimens were preserved in 70% ethyl alcohol. The fifth instar is described in detail but only major differences are described for preceeding instars. Measurements are given in mm as mean ± SD. Length was measured from apex of vertex to terminus of abdomen, thoracic length along the midline from anterior margin of the pronotum to posterior margin of the metanotum, and width across the widest part of the body. Specimens of each nymphal instar were cleared in 6% KOH in order to examine distribution and number of body pits.

Eggs were obtained by dissecting them out of a leaf of *Spartina* sp. Pieces of *Spartina*
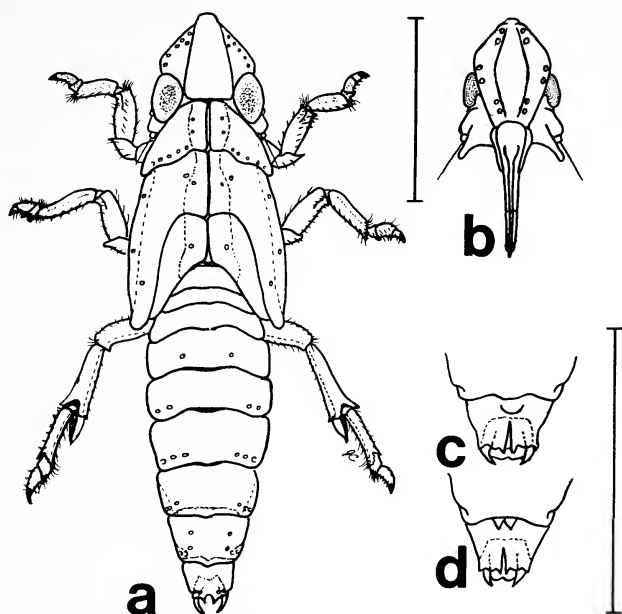
Fig. 1. *N. elongatus* fifth instar. a. Habitus. b. Frontal view of head. c. Ventral view of apex of abdomen of male. d. Ventral view of apex of abdomen of female. Bars = 0.5 mm.

sp. leaves were placed on filter paper in petri dishes in the laboratory. First instars hatched from eggs embedded in these leaves. Second through fifth instars and adults were collected by sweeping the host plants. The data for specimens collected for this study are: FLORIDA: Broward Co., Ft. Lauderdale, 12 December 1985, coll. P. Calvert, ex. *Spartina patens,* 16 male macropters, 24 female brachypters, 20 fifth, 40 fourth, 18 third, 8 second, and 9 first instars, and 2 eggs.

Fifth instar (Fig. 1a). Length 3.07 ± 0.173; thoracic length 0.92 ± 0.035; width 0.69 ± 0.042 (N = 20).

Form elongate, subcylindrical, slightly flattened dorsoventrally, widest across mesothoracic wingpads. Body whitish with no distinguishing coloration; legs white, tarsi with dark brown to black apices.

Head conical. Vertex elongate, triangular, posterior margin almost straight with rounded corners narrowing anteriorly, lateral margins straight, smooth; carina on each side extending anteromedially from inner margin of compound eye and continuing onto frons as inner carina. Frons widest in posterior ⅓; lateral margins convex and carinate (outer carinae), extending from vertex to near clypeal border and paralleled by pair of inner carinae; 5–7 pits on gena between each frontal outer carina and eye. Clypeus narrowing distally, consisting of subconical basal postclypeus and cylindrical distal anteclypeus. Beak extending almost to bases of metacoxae; 3-segmented, segment 1 obscured by anteclypeus, segment 2 ca. 1.5× length of segment 3, segment 3 with black apex. Eyes red. Antennae 3-segmented; scape cylindrical, slightly longer than wide; pedicel subcylindrical, ca. 4× length of scape, with 5–8
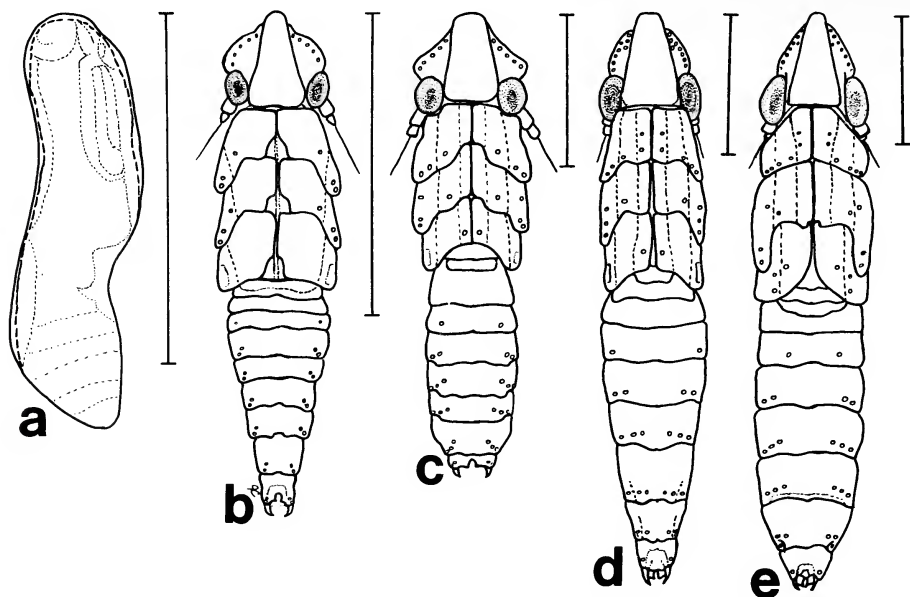
Fig. 2.   *N. elongatus* immatures. a. Egg. b. First instar. c. Second instar. d. Third instar. e. Fourth instar. Bars = 0.5 mm.

pitlike sensoria; flagellum bulbous basally, with elongate, bristle-like extension distally, bulbous base ca. $0.25 \times$ length of pedicel.

Thoracic nota divided by middorsal line into three pairs of plates. Pronotal plates subrectangular; anterior margin following posterior margin of vertex and eye, posterior border sinuate; each plate with slightly curved, oblique posterolaterally directed carina originating on anterior margin in median $\frac{1}{3}$ and terminating in lateral $\frac{1}{3}$; area between carinae elevated and subtriangular; carina bordered along inner margin by row of 7 pits extending posterolaterally to lateral border of plate (lateralmost pits not visible in dorsal view). Mesonotal median length ca. $1.5-2\times$ that of pronotum; each plate bearing an elongate lobate wingpad extending nearly to apex of metanotal wingpad; with 2 weak longitudinal carinae, inner carina originating on anterior margin in median $\frac{1}{4}$ and terminating on posterior margin in median $\frac{1}{3}$, outer carina originating on anterior margin in lateral $\frac{3}{4}$, paralleling lateral border and terminating on posterior margin; area between inner carinae elevated; 2 pits near inner carina and 3 pits in lateral $\frac{1}{3}$. Metanotal median length subequal to that of mesonotum; each plate bearing an elongate lobate wingpad extending almost to anterior margin of tergite 3; with posterolaterally directed carina originating on anterior margin in median $\frac{1}{4}$ and terminating on posterior margin in lateral $\frac{1}{2}$; 1 pit in middle of each plate. Pro- and mesocoxae elongate, posteromedially directed; metacoxae fused to sternum. Metatrochanter short and subcylindrical. Pro- and mesofemora and tibiae each with 2 ventral longitudinal rows of setae. Metatibia with 2 black-tipped spines on lateral aspect of shaft, an apical transverse row of 5 black-tipped spines on ventral
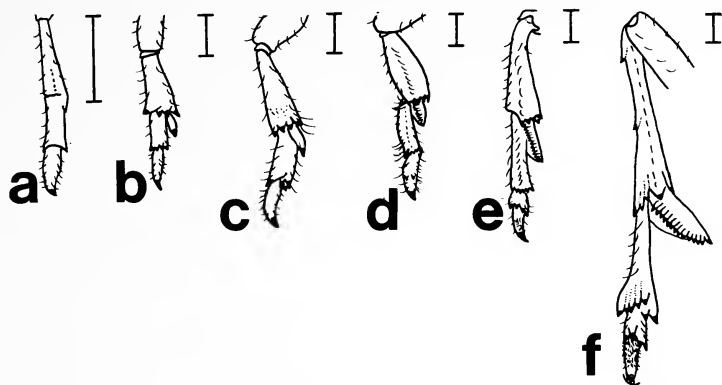
Fig. 3. *N. elongatus* apices of metathoracic legs, plantar surface. a. First instar. b. Second instar. c. Third instar. d. Fourth instar. e. Fifth instar. f. Adult. Bars = 0.1 mm.

aspect and a subtriangular, flattened movable spur with row of 10–13 teeth on posterior margin. Pro- and mesotarsi with 2 tarsomeres; tarsomere 1 wedge-shaped; tarsomere 2 subconical, curved, ca. 3× length of tarsomere 1 and with pair of apical claws and median membranous pulvillus. Metatarsi with 3 tarsomeres; tarsomere 1 cylindrical with apical transverse row of 6–7 black-tipped spines on plantar surface; tarsomere 2 cylindrical, ca. 0.25× length of tarsomere 1, with apical transverse row of 4 black-tipped spines on plantar surface; tarsomere 3 subconical, ca. 1.5× length of tarsomere 2 and with pair of apical claws and median pulvillus.

Abdomen 9 segmented; slightly flattened dorsoventrally, widest across 5th abdominal segment. Tergite 1 small, subtriangular; 2 subtriangular, 2.3× width of 1; tergites 4–8 with following number of pits on either side of midline (lateralmost pits not visible in dorsal view in some cases due to curving of tergites onto ventral aspect): tergite 4 with 1, 5 with 1–2, 6 with 3, 7 with 3, 8 with 3. Segment 9 surrounding anus; with 3 pits on each side; female with 1 pair of subacute dark brown processes extending caudally from juncture of sternites 8 and 9; males lacking processes.

Fourth instar (Fig. 2e). Length 2.56 ± 0.150; thoracic length 0.70 ± 0.190; width 0.52 ± 0.028 (N = 20).

Antennal pedicel with 5–8 pitlike sensoria. Flagellum ca. .25× length of pedicel.

Pronotal pits very obscure, nearly invisible in some specimens. Mesonotal wingpads shorter, covering ⅔ of metanotal wingpad laterally. Mesonotal median length subequal to that of mesonotum; carinae weaker; wingpad extending to tergite 2. Metatibial spur slightly smaller, with 4 teeth on margin. Metatarsi with 2 tarsomeres; tarsomere 1 with apical transverse row of 6 black-tipped spines on plantar surface; tarsomere 2 subconical, partially subdivided, with 2 black-tipped spines in middle of plantar surface.

Abdominal tergites with the following number pits on either side of midline (lateralmost pits not visible in dorsal view due to curving of tergites onto ventral aspect): tergite 4 with 1, 5 with 2, 6 with 3, 7 with 3, 8 with 3.

Third instar (Fig. 2d). Length 1.98 ± 0.130; thoracic length 0.59 ± 0.027; width 0.39 ± 0.040 (N = 18).

Antennal pedicel with 4 very weak pitlike sensoria; bulbous portion of flagellum subequal to length of pedicel.

Pronotal plates each with row of 4 pits. Mesonotal wingpads shorter, covering ⅓ of metanotal wingpad laterally. Metanotal wingpad extending to juncture of tergites 1 and 2. Metatibial spur smaller, with 2 teeth on margin. Metatarsomere 1 with apical transverse row of 4 black-tipped spines on plantar surface; tarsomere 2 lacking spines.

Abdominal tergites with the following number of pits on either side of midline (lateralmost pits not visible in dorsal view due to curving of tergites onto ventral aspect): tergite 4 with 1, 5 with 2, 6–8 with 2–3.

Second instar (Fig. 2c). Length 1.45 ± 0.820; thoracic length 0.42 ± 0.016; width 0.24 ± 0.016 (N = 8).

Frons with 5 pits between outer carina and eye. Antennal pedicel apparently lacking sensoria.

Mesonotal plates each with 4 pits; wingpads not developed. Metanotal wingpads not developed. Metatibia with apical transverse row of 4 black-tipped spines on plantar surface; spur much smaller, ca. 2× length of longest metatibial spine, without marginal teeth, with black-tipped tooth at apex. Abdominal tergites with the following number of pits on either side of midline (lateralmost pits not visible in dorsal view due to curving of tergites onto ventral aspect): tergite 4 with 1, 5 with 2, tergite 6–8 with 3.

First instar (Fig. 2b). Length 1.02 ± 0.080; thoracic length 0.33 ± 0.018; width 0.19 ± 0.013 (N = 9).

Body and legs white; pits very obscure.

Pronotal plates each with 3–4 pits. Mesonotal plates with 3 pits. Metanotal plates with weak ridges on lateralmost edge. Metatibia lacking lateral spines on shaft; spur not developed.

Abdominal tergite 4 with 1 pit and 5–8 each with 2 pits.

Egg (Fig. 2a). Length 0.65; width 0.18 (N = 2).

Egg ovoid, white (in alcohol), chorion smooth.

KEY TO NYMPHAL INSTARS

1. Metatarsi with 3 tarsomeres or with tarsomere 2 partially subdivided and bearing 2 weak spines in middle on plantar surface (Fig. 3d, e) 2
– Metatarsi with 2 tarsomeres; tarsomere 2 lacking spines (Fig. 3a–c) 3
2. Metatibial spur with 10 or more teeth; metatarsi with 3 tarsomeres, tarsomere 2 with apical transverse row of 4 spines (Fig. 3e) .... Fifth instar
– Metatibial spur with 4 teeth; metatarsi with 2 tarsomeres, tarsomere 2 partially subdivided and with 2 weak spines in middle (Fig. 3d) .... Fourth instar
3. Metatibial spur with 2 marginal teeth and 1 apical tooth (Fig. 3c) ....Third instar
– Metatibial spur lacking marginal teeth, with 1 apical tooth (Fig. 3a, b) 4
4. Metatibial spur ca. 2× length of longest metatibial spine (Fig. 3b); metatibia with 2 lateral spines on shaft .... Second instar
– Metatibial spur less than 2× length of longest metatibial spine (Fig. 3a); metatibia lacking lateral spines on shaft .... First instar

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NOTES ON THE BIOLOGY AND IMMATURES OF THE ISSID PLANTHOPPERS *THIONIA BULLATA* AND *T. SIMPLEX* (HOMOPTERA: FULGOROIDEA)

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Abstract.—Observations on host plants and descriptions of nymphs of *Thionia bullata* (Say) and *T. simplex* (Germar) are provided. *T. bullata* was recorded from three species of pines in Alabama and *T. simplex* from 12 species of herbaceous and woody dicotyledonous plants from North Carolina, Pennsylvania, Tennessee, and District of Columbia. Salient features of nymphs include number and arrangement of body pits, spination of the metathoracic legs, and form of the abdominal waxpads.

The issid genus *Thionia* Stål contains 72 mostly neotropical planthoppers (Metcalf, 1958; Fennah, 1965; Wheeler and Wilson, 1987). Little ecological information is available for the 8 species found north of Mexico. These species are usually poorly represented in collections with some of the eastern species characterized as "rare" or "quite rare" (e.g., Dozier, 1926; Osborn, 1938). Only *T. elliptica* (Germar) has been studied in any detail; Wheeler and Wilson (1987) reported its seasonal history on scrub oak, *Quercus ilicifolia* Wang., in Pennsylvania and described and illustrated the immature stages.

Thionia bullata (Say) is recorded from Pennsylvania and New Jersey west to Illinois and south to Mississippi and Florida (Metcalf, 1958; Wilson and McPherson, 1980a). This planthopper has been taken on oak (*Quercus* sp.) in Mississippi, where nymphs and adults were said to be abundant at many localities (Dozier, 1926), and on dogwood (*Cornus* sp.) and river weeds in Indiana (Heaton, 1934). Wilson and McPherson (1979) listed *T. bullata* as a host of the parasitic moth *Fulgoraecia exigua* (Hy. Edwards) (=*Epipyrops barberiana* Dyar) (Lepidoptera: Epipyropidae) in Illinois.

Thionia simplex (Germar) has a recorded distribution similar to that of *T. bullata* (Metcalf, 1958; Wilson and McPherson, 1980a). Adults have been swept from a grassy field in Florida (Van Duzee, 1909) and "low deciduous woods" in Mississippi (Dozier, 1926). Hook (1981) reported the wasp *Tanyoprymnus moneduloides* (Packard) (Hymenoptera: Sphecidae) provisioning its nest with *T. simplex* in Georgia.

Here we record host plants for *T. bullata* and *T. simplex,* describe and illustrate nymphal instars of both species, and compare them with those of *T. elliptica.* The host records are based on field observations by AGW; nymphal descriptions were made by SWW.

MATERIALS AND METHODS

Specimens, including nymphs used in the descriptions, were collected by A. G. Wheeler, Jr. (or G. L. Miller—indicated as GLM) at the following localities and dates:

T. bullata—ALABAMA: Clay Co., Rt. 9, Barfield, 11 May 1986, ex. *Pinus taeda,* 3 fifth, 7 fourth, 3 third instars; Conecuh Co., County Rt. 29 at Sepulga R. s. of Deans, 10 May, ex. *Pinus taeda,* 4 fifth instars; nr. Owassa, 10 May, ex. *Pinus echinata* and *P. taeda,* 1 fifth, 1 fourth instar; Lee Co., Auburn, Auburn University Campus, 11 May, ex. *Pinus virginiana,* 11 fifth instars, 4 male, 1 female adult; 6 June, ex. *Pinus virginiana,* 1 male, 6 female adults (GLM); Montgomery Co., I-85 s. of Macon Co. line nr. Waugh, 10 May, ex. *Pinus taeda,* 8 fifth instars; Tallapoosa Co., Rt. 280 and Rt. 50, Camp Hill, ex. *Pinus echinata,* 1 fifth, 4 fourth instars; ex. *Pinus taeda,* 6 fifth instars; Tuscaloosa Co., Tuscaloosa, 8 June 1987, ex. *Pinus echinata,* 2 males. *T. simplex*—NORTH CAROLINA: Mecklenburg Co., Charlotte, 4 June 1983, ex. *Elaeagnus multiflora,* 3 second, 1 first instar; 3 July 1982, ex. *Elaeagnus* sp., 7 fifth, 2 fourth instars, 1 male adult; ex. *Baccharis halimifolia,* 1 female adult; ex. privet, 1 male adult; 2 July 1983, on various tree and shrub species, 5 fifth, 6 fourth, 1 third instar; 7 July 1984, ex. *Baccharis halimifolia,* 1 male adult; 4 September 1983, ex. *Baccharis halimifolia,* 1 male adult; PENNSYLVANIA: York Co., Shenks Ferry, ex. *Physalis* sp., 22 July 1981; TENNESSEE: Knox Co., Knoxville, University of Tennessee campus, 16 July 1982, ex. *Elaeagnus* sp., 2 fifth instars; WASHINGTON, D.C.: National Arboretum, 17 July 1983, ex. *Solanum carolinense* and *S. dulcamera,* late instar nymphs (not collected).

Nymphs were preserved in 70% ethyl alcohol. Measurements are given in mm as Mean ± SD. Length was measured from apex of vertex to apex of abdomen for nymphs, thoracic length along the midline from the anterior margin of the pronotum to the posterior margin of the metanotum, and width across the widest part of the body. At least one specimen of each instar was cleared in 10% cold KOH then immersed in water; this allowed for determination of the number and arrangement of pits and waxpads. In each of the instars, the lateralmost pits on the tergites are not always visible in dorsal view due to curving of the tergites onto the ventral aspect. The five nymphal instars of *T. elliptica* were described in detail by Wheeler and Wilson (1987); the following descriptions include those features that distinguish nymphs of *T. bullata* and *T. simplex* from those of *T. elliptica.*

RESULTS AND DISCUSSION

Thionia bullata (Say)

Host plants. In Alabama, *T. bullata* was collected from three species of pines from 10–12 May 1986 (Table 1). Late instars were beaten from loblolly pine, *Pinus taeda* L., and shortleaf pine, *P. echinata* Mill., in Clay, Conecuh, Montgomery, and Tallapoosa counties. Nymphs were particularly numerous on loblolly pine in the Red Hills region of Conecuh Co. Late instars, many with attached epipyropid larvae, were common on an isolated scrub pine, *P. virginiana* Mill., in Lee Co. on the Auburn University campus; a few teneral adults also were present.

Our discovery that pines serve as host plants is difficult to reconcile with Dozier's (1926) and Heaton's (1934) reports and suggests misidentifications of their planthoppers or observation of planthoppers resting on plants but not necessarily feeding.

Descriptions. FIFTH INSTAR (Fig. 1a–c). Length 5.0 ± 0.58; thoracic length 2.2 ± 0.09; width 3.3 ± 0.30. N = 34.

Body light brown to tan dorsally, intermittent orange longitudinal markings ex-

Table 1.   Host plants of *Thionia bullata* and *T. simplex*.

Taxon	Common name	Stage[a]	Locality[b]
Thionia bullata			
Pinaceae			
Pinus taeda L.	loblolly pine	N	AL
Pinus echinata Mill.	shortleaf pine	N	AL
Pinus virginiana Mill.	Virginia pine	N, A	AL
Thionia simplex			
Altingiaceae			
Liquidambar styraciflua L.	sweetgum	N	NC
Anacardiaceae			
Rhus copallina L.	winged sumac	N	NC
Asteraceae			
Baccharis halimifolia L.	sea myrtle	N, A	NC
Elaeagnaceae			
Elaeagnus multiflora Thunb.	cherry eleagnus	N, A	NC
Fabaceae			
Albizia julibrissin Durazz.	mimosa	N	NC
Magnoliaceae			
Magnolia grandiflora L.	southern magnolia	N	NC
Oleaceae			
Ligustrum amurense Carr.	Amur privet	N, A	NC
Rosaceae			
Prunus sp.	cherry	N	NC
Solanaceae			
Physalis sp.	ground cherry	N	PA
Solanum carolinense L.	horsenettle	N	DC
Solanum dulcamara L.	bitter nightshade	N	DC
Ulmaceae			
Ulmus alata Michx.	winged elm	N	NC

[a] N = nymph, A = adult.
[b] AL = Alabama; DC = Washington, D.C.; NC = North Carolina; PA = Pennsylvania; see text for detailed collection records.

tending from posterior margin of vertex across thorax and abdominal tergites 1–6. Venter pale tan with light to medium brown markings.

Vertex length subequal to width, anterior margin carinate, subacute; appearing pentagonal. Frons slightly longer than wide, anterodorsal margin arcuate, lateral margins strongly convex and carinate (outer carinae), paralleled by inner carina on each side, median longitudinal carina fading in posterior half; 34–39 pits between each inner and outer carina. Eyes red without pale stripes. Antennal pedicel ca. 4× length of scape.

Mesonotal plates each with cluster of 9–11 pits just lateral to carina and 9–11 pits on wingpad. Metanotal plates each with weak longitudinal carina originating on anterior margin in median ⅓, curving mesad then fading in posterior ⅓ of plate. Metatibiae with longitudinal row of 3 lateral spines on shaft and transverse apical row of 8–9 spines on plantar surface. Metatarsomere 1 with transverse apical row of 6–9 spines (generally 8) apically on plantar surface; tarsomere 2 with 2 apical spines.

Abdominal segments 8–9 telescoped anteriorly; tergites 7 and 8 each with a pair of elongate, oval, white caudal waxpads; those on tergite 7 are hidden on the ventral aspect and are only readily apparent if the specimen is cleared. Tergites each with the following number of pits on either side of midline: tergite 3 with 5–6 pits, 4 with 7–8, 5 with 8, 6 with 8, 7 with 8–9, and 8 with 5–7.

FOURTH INSTAR. Length 3.4 ± 0.30; thoracic length 1.5 ± 0.05; width 2.0 ± 0.08. N = 12.

Frons with 30–32 pits between each inner and outer carina. Antennal pedicel ca. 3× length of scape, bulbous portion of flagellum ca. 0.25 length of pedicel; pedicel with ca. 10 very obscure pits.

Pronotal plates each with ca. 25–26 pits in 3 irregular rows. Mesonotal plates each with 8–9 pits just lateral to carina and 8 laterally on wingpad; wingpad broadly lobate and covering ca. ½ metanotal wingpad laterally. Metanotal wingpad with 4 pits in lateral ⅓ and 3 laterally on wingpad. Metatibiae with apical transverse row of 8 spines on plantar surface. Metatarsomere 1 with apical transverse row of 7 spines on plantar surface.

Abdominal tergites each with the following number of pits on either side of midline: tergite 3 with 5 pits, 4 with 6–7, 5 with 7, 6 with 6–7, 7 with 6–7, 8 with 5.

THIRD INSTAR. Length 2.5 ± 0.06; thoracic length 1.1 ± 0.17; width 1.5 ± 0.12. N = 3.

Frons with ca. 25–26 pits between each inner and outer carina. Antennal pedicel with fewer very obscure pits.

Pronotal plates each with 23–25 pits in 3 irregular rows. Mesonotal plates each with 6–7 pits just lateral to carina and 7 pits in lateral ⅓. Metanotal plates each with 3 very obscure pits just lateral to carina and 3 pits in lateral ⅓. Metatibiae with an apical transverse row of 6 spines on plantar surface. Metatarsi with 2 tarsomeres; tarsomere 1 cylindrical, with an apical transverse row of 6 spines on plantar surface.

Abdominal tergites each with the following number of pits on either side of midline: tergite 3 with 3 pits, 4–7 each with 5, 8 with 3.

Thionia simplex (Germar)

Host plants. T. simplex was collected from 12 host plant species in 10 families (Table 1). Nymphs collected in Washington, D. C. were observed feeding on stems and lower leaf surfaces of bitter nightshade, *Solanum dulcamara* L., and horsenettle, *S. carolinense* L.

The collection of *T. simplex* on various herbs, shrubs, and trees appears to contrast with *T. elliptica,* which has been taken only on oaks (Wheeler and Wilson, 1987), and *T. bullata,* an apparent pine feeder. *Thionia simplex* thus is polyphagous like several other eastern North American planthoppers: the acanaloniines *Acanalonia bivittata* (Say) and *A. conica* (Say) (Wilson and McPherson, 1980b, 1981a); flatids
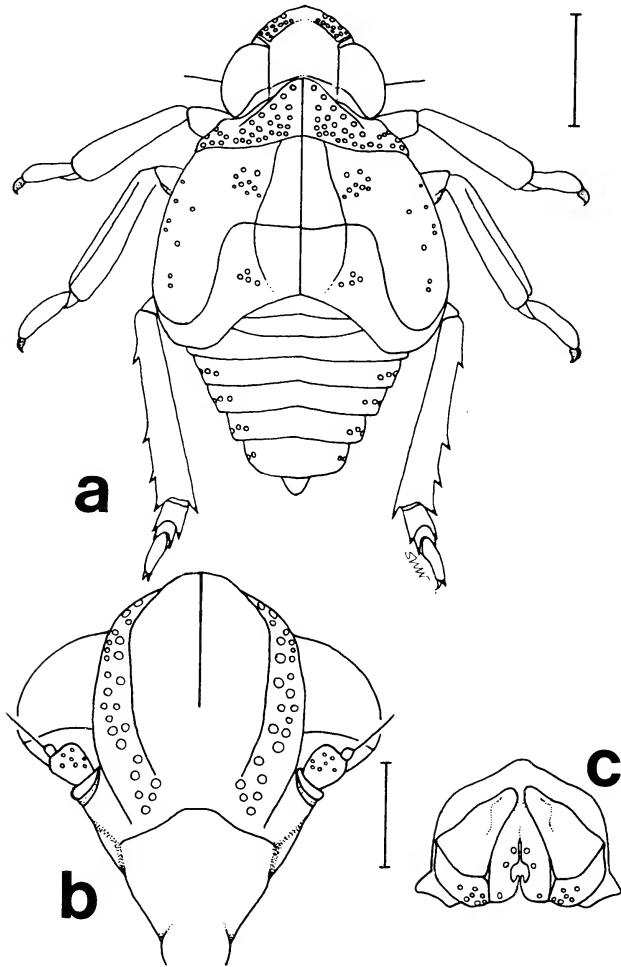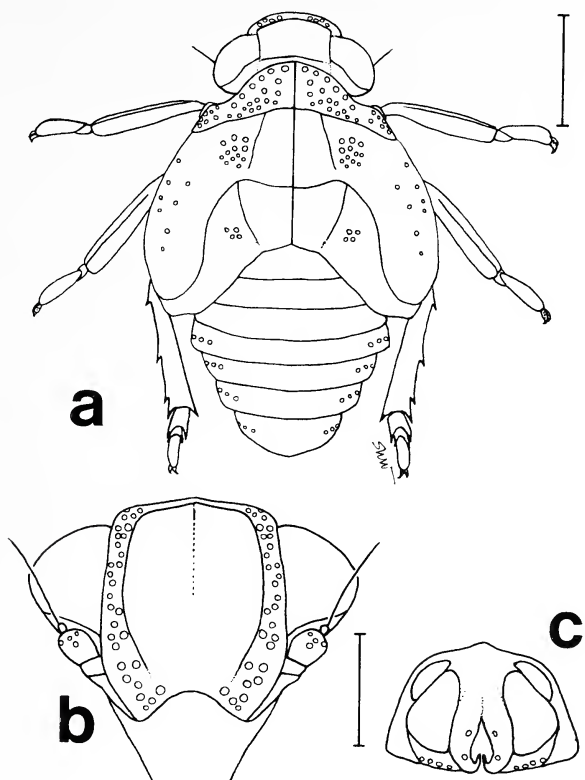
Fig. 1.   *T. bullata* fifth instar. a. Habitus. b. Frontal view of head. c. Caudal view of abdomen. Bar = 1 mm (a); 0.5 mm (b, c).

Anormenis chloris (Melichar) (=*septentrionalis* (Spinola); see O'Brien, 1985), *Metcalfa pruinosa* (Say), *Ormenaria rufifascia* (Walker) and *Ormenoides venusta* (Melichar) (Wilson and McPherson, 1980b, 1981b; Wilson and Tsai, 1984) and *Cyarda* sp., near *acutissima* Metcalf and Bruner (Wheeler and Hoebeke, 1982); and tropiduchid *Pelitropis rotulata* Van Duzee (Wilson and Wheeler, 1984).

Descriptions. FIFTH INSTAR (Fig. 2a–c). Length 5.0 ± 0.91; thoracic length 1.7 ± 0.06; width 3.0 ± 0.27; N = 14.

Body light tan; very faint, brownish longitudinal stripes dorsally.

Vertex length ca. 0.7× width; anterior margin carinate and arcuate, lateral margins carinate, posterior margin concave. Frons with weak median longitudinal carina fading in posterior ⅓; 36–40 pits between each inner and outer carina. Eyes red

Fig. 2.   *T. simplex* fifth instar. a. Habitus. b. Frontal view of head. c. Caudal view of abdomen.
Bar = 1 mm (a); 0.5 mm (b, c).

without pale stripes. Antennal pedicel with numerous obscure pits, ca. 4× length of
scape.

Pronotal plates each with 26–29 pits in 4 irregular rows. Mesonotal plates each
with straight longitudinal carina originating on anterior margin in median ¼ and
extending posterolaterally to posterior margin; cluster of 11–12 pits just lateral to
carina and 9 pits on wingpad. Metanotal plates each with weak longitudinal carina
originating on anterior margin in median ⅓ and fading in posterior ¼; 3–5 pits just
lateral to carina. Metatibiae with longitudinal row of 3 lateral spines on shaft and
transverse apical row of 8–10 spines on plantar surface. Metatarsomere 1 with trans-
verse apical row of 8–9 spines apically on plantar surface.

Abdominal segments 8–9 telescoped anteriorly; tergites 7 and 8 each with a pair
of elongate, oval, white caudal waxpads; those on tergite 7 are hidden on the ventral
aspect and are only readily apparent if the specimen is cleared. Tergites each with
the following number of pits on either side of midline: tergite 3 with 5 pits, 4 with
7–8, 5 with 7, 6 with 8, 7 with 7–8, and 8 with 5–6.

FOURTH INSTAR. Length 3.7 ± 0.37; thoracic length 1.3 ± 0.03; width 1.9 ±
0.08. N = 8.

Frons with 30–32 pits between each inner and outer carina. Antennal pedicel ca. $3\times$ length of scape; bulbous portion of flagellum ca. $0.25\times$ length of pedicel; fewer obscure pits on pedicel.

Pronotal plates each with 26–27 pits in 3 irregular rows. Mesonotal plates each with 10 pits just lateral to carina; wingpad broadly lobate and covering ca. ½ metanotal wingpad laterally. Metanotal plates each with 4 pits just lateral to carina and 4 pits on wingpad in lateral ⅓. Metatibial shaft with 2–3 lateral spines; apical transverse row of 6–8 spines on plantar surface. Metatarsomere 1 with apical transverse row of 7–8 spines on plantar surface.

Abdominal tergites each with the following number of pits on either side of midline: tergite 3 with 5 pits, 4 with 6–7, 5 with 6, 6 with 7, 7 with 7, 8 with 4.

THIRD INSTAR. Length 2.7; thoracic length 0.9; width 1.2. N = 1.

Frons with ca. 20 pits between each inner and outer carina. Antennal pedicel ca. $3\times$ length of scape; bulbous portion of flagellum ca. $0.5\times$ length of pedicel.

Pronotal plates each with 23 pits in 3 irregular rows. Mesonotal plates each with 7–8 pits just lateral to carina and 6 pits on wingpad in lateral ⅓. Metanotal plates each with 1 very obscure pit just lateral to carina and 3 pits on wingpad in lateral ⅓. Metatibial shaft with 2–3 (if with 3, then third very weak) lateral spines; apical transverse row of 6 spines on plantar surface. Metatarsi with 2 tarsomeres; tarsomere 1 with apical transverse row of 6 spines on plantar surface.

Abdominal tergites each with the following number of pits on either side of midline: tergite 3 with 3 pits, 4 with 5, 5 with 5, 6 with 5, 7 with 4, 8 with 3.

SECOND INSTAR. Length 1.6 ± 0.13; thoracic length 0.7 ± 0.01; width 0.9 ± 0.08. N = 3.

Frons with 16 pits between each outer and inner carina. Antennal pedicel ca. $2\times$ length of scape.

Pronotal plates each with 17–18 pits in 2 distinct transverse rows. Mesonotal plates each with group of 5 pits just lateral to carina and 4 pits on wingpad in lateral ⅓. Metanotal plates each with 2 pits on wingpad in lateral ⅓. Metatibia with 2 lateral spines on shaft and an apical transverse row of 5 spines on plantar surface. Metatarsomere 1 with an apical transverse row of 5 spines on plantar surface.

Abdominal tergites each with the following number of pits on either side of midline: tergite 3 with 1 pit, 4–7 each with 3 pits, 8 apparently with 1 pit.

FIRST INSTAR. Length 1.6; thoracic length 0.45; width 0.65. N = 1.

Frons with 11 pits between each outer and inner carina.

Pronotal plates each with 11 pits in distinct transverse row. Mesonotal plates each with group of 2 pits just lateral to carina and 2 pits on wingpad in lateral ⅓. Metanotal plates each with 1 pit on wingpad in lateral ⅓. Metatibia without lateral spines on shaft; apical transverse row of 4 spines on plantar surface. Metatarsomere 1 with an apical transverse row of 4 spines on plantar surface.

Abdominal tergites each with the following number of pits on either side of midline: tergite 3 without pits, 4–7 each with 3 pits, 8 apparently with 1 pit.

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A NEW GENUS OF FOAM-INHABITING VELIIDAE (HETEROPTERA) FROM WESTERN MADAGASCAR

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Abstract.—A new genus of Microveliinae, *Aphrovelia,* is described on the basis of a new species, *A. phoretica,* from several localities in western Madagascar. The unusual habits of this species, which occurs on rafts of foam along the banks of sandy rivers, are discussed. Illustrations of key characters and a discussion of the relationship of this new genus to allied genera of Microveliinae are provided.

While making collections of aquatic Heteroptera during a recent National Geographic Society expedition to Madagascar we discovered a new genus of Microveliinae, for which we propose the name *Aphrovelia,* at two widely separated localities in the dry western portion of the island. The most remarkable characteristic of these veliids is their habit of living on rafts of river foam trapped by tangles of logs and sticks. This habitat is reminiscent of that described by Spangler (1986) for *Oiovelia spumicola* Spangler in Venezuela, however the insects of the genus described here were not observed to enter the foam as reported for the latter, but instead aggregated on the surface of it. A diligent but fruitless search for *Aphrovelia* in alternative microhabitats suggests that this genus is indeed restricted to the foam habitat. As far as we are aware, the only other veliid recorded from foam is *Pseudovelia gnoma* Polhemus from Ceylon (Andersen, 1983). Since *Aphrovelia* and *Oiovelia* are not closely related genera and are widely separated geographically, we conclude that the spumicolous habit has evolved independently at least twice in the Veliidae.

All measurements are given in millimeters. CL numbers following locality data refer to codes used by the authors to reference ecological data. Specimen repository abbreviations are as indicted in the acknowledgments.

Aphrovelia, new genus
Figs. 1–13

Description. Eyes triangular in side view; not exserted but nearly conforming to the head curvature (Figs. 1–4); not touching thorax posteriorly; anteriorly separated from the glabrous antennal tubercle (socket) by the width of antennal segment II; densely hirsute, setae curved, tips directed anteriorly (Fig. 11). Gular region long, bucculae not well developed (Fig. 7). Female pronotum strongly constricted anteriorly (Figs. 1–2). Female abdomen essential flat dorsally, with tergites and connexiva on one plane, connexiva not raised. Male hind tibia curved and modified distally (Fig. 10) to facilitate phoresy. Tarsal formula 1:2:2. Fore wings with four closed cells, veins extending onto distal quarter (Fig. 2). Male parameres small, not well developed. Female gonapophysis 1 lanceolate. Most other characteristics as in the genus *Pseudovelia.*

Discussion. Aphrovelia phoretica clearly belongs in the subfamily Microveliinae
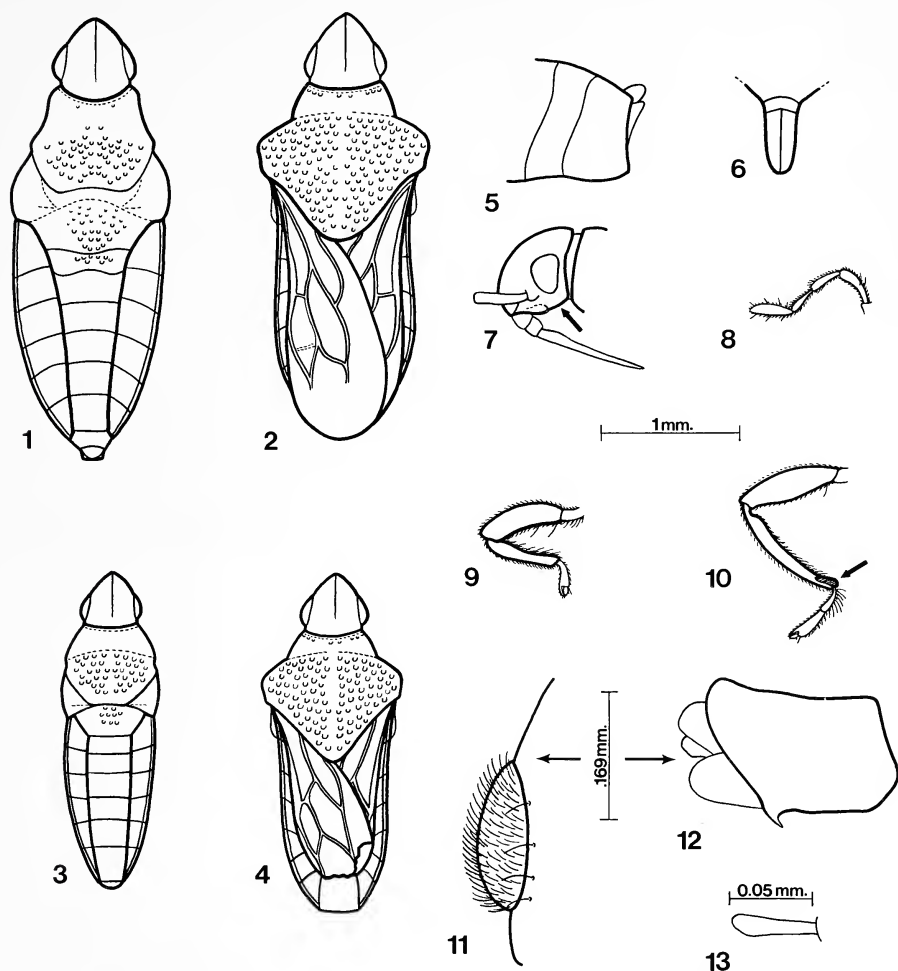
Figs. 1–13. *Aphrovelia phoretica.* 1. Apterous female, habitus. 2. Macropterous female, habitus. 3. Apterous male, habitus. 4. Macropterous male, habitus. 5. Female abdominal terminalia, lateral view. 6. Female abdominal terminalia, caudal view. 7. Head, lateral view, showing long gula (arrow). 8. Antenna. 9. Male fore leg. 10. Male posterior leg, showing distal tibial pad for grasping female in phoresy (arrow). 11. Eye, dorsal view, showing setiferation. 12. Male genital segments. 13. Male paramere.

based on wing venation, tarsal formula, leg structure and absence of ocelli. In Andersen's key (1982, pp. 418–421) to the genera of Veliidae *Aphrovelia* keys to *Microvelia,* but differs from the latter by the characteristics summarized in the table below. The fore wing venation does not extend distally as far as in *Microvelia,* but on the other hand is not truncate as in *Pseudovelia,* and is thus intermediate between these two genera. In general habitus, length of the first antennal segment, long male fore tibial comb and distally truncate female abdomen *Aphrovelia phoretica* more

Table 1.   Characters for separation of *Aphrovelia, Microvelia,* and *Pseudovelia.*

Character	Aphrovelia	Microvelia	Pseudovelia
Eye shape, side view	triangular	globular	triangular-globular
Eyes exserted	no	yes	yes
Eyes hirsute	yes	no	no (but see discussion)
Hind margin of eye touching thorax	no	yes	yes
Anterior margin of eye touching antennal tubercle	no	yes	yes
Gula, length	long	moderate	short to moderate
Male with patch of dark hairs distally on hind tibia	yes	no	yes, in a few species
Female thorax abruptly narrowed anteriorly	yes	no	no
Female abdomen essentially flat dorsally	yes	no	no

closely resembles *Pseudovelia* than *Microvelia.* The wing venation and head characteristics will separate these genera as will most of the characters in the table above. We have compared *Aphrovelia* to most of the described species and 23 undescribed species of *Pseudovelia,* and the only two we have seen that share several key characteristics are *P. feuerborni* (Lundblad) from Sumatra and southeast Asia and *P. betiokyi perineti* Poisson from Madagascar, both of which have a pad of densely set setae on the male hind tibia (but not as densely packed as in *Aphrovelia*), and a simple male first genital segment without adorning spines or projections ventrally. We believe the simple male genitalia are plesiomorphic, but the nature of the head and eyes in *Aphrovelia* (given in Table 1) constitute a strong synapomorphy separating it from *Pseudovelia.* Several *Pseudovelia* species have hirsute eyes, but only those species with a body covering of long setae, and the eye setae are not curved forwardly as in *Aphrovelia phoretica.* The longitudinally arched male body, strongly curved male hind femora terminating in a distinct grasping pad, anteriorly strongly narrowed female pronotum, and essentially flat dorsal surface of the female abdomen may also be synapomorphies for *Aphrovelia,* but more species will be needed to test this.

Type-species. Aphrovelia phoretica J. & D. Polhemus

Etymology. The generic name is derived from *Aphros,* Gr., foam, pertaining to the peculiar habitat of these insects.

Distribution. Western Madagascar, Tulear and Majunga provinces.

Aphrovelia phoretica, new species
Figs. 1–13

Description. Apterous female: Ground color black, heavily marked with orange brown; broad quadrate area anteriorly, irregular median area of posterior lobe, posterior margin of pronotum, abdominal tergites III–VI medially, connexival margins, upper mesopleura, most of prosternum, acetabulae, abdominal sternites except midlateral longitudinal stripe, orange brown. Legs leucine to testaceous, tarsal tips black.

Vertex of head along eyes, abdominal tergites except median areas of tergites I–V, connexiva dorsally, metapleura above acetabulae, with coarse silvery pubescence.

Structural characteristics: Head long, declivant anteriorly; eyes of moderate size, not exserted, thickly set with curved forwardly directed setae (Fig. 11); not touching thorax posteriorly; anteriorly separated from the glabrous antennal tubercle (socket) by the width of antennal segment II; interocular space very wide, about 6 times the width of an eye. Antennae moderately long, moderately stout; length of segments I–IV: 0.43: 0.36: 0.29: 0.43. Pronotum long, narrow, slightly laterally expanded posteriorly; posterior margin truncate, covering mesonotum and metanotum medially; length on midline, 0.65. Mesothorax broad (Fig. 1), abruptly tapering anteriorly to narrower prothorax, entire complex forming a broad shallow sulcus for reception of male forelegs in phoresy. Abdominal tergite 1 long (0.40), II–VII subequal in length (0.18–0.22); connexiva not raised but coplanar with abdominal tergites, abdominal dorsum essentially flat. Legs relatively stout, not significantly modified in female; middle tibia beneath with a row of about 9–10 evenly spaced slender erect long setae curved only at tip.

Proportions of legs as follows:

	Femur	Tibia	Tarsal 1	Tarsal 2
Anterior	0.79	0.72	0.43	—
Middle	1.04	0.97	0.22	0.40
Posterior	1.26	1.30	0.22	0.43

Pregenital abdomen truncate (Fig. 5), gonocoxae elongate (Fig. 6). Female gonapophysis 1 lanceolate. Length, 3.38 mm.; width, 1.22 mm.

Macropterous female: Structure and coloration mostly as in apterous form. Pronotum covering wing bases, abruptly narrowed anterad of humeri (Fig. 2); broadly orange brown medially and posteriorly, humeri orange brown. Wing venation typical of Microveliinae; hemelytra white basally, gradually becoming smoky grey brown distally, without light spots; veins prominent, dark. Length, 3.28 mm; width, 1.26 mm.

Apterous male: Much smaller and narrower than female, without constricted thorax (Fig. 3). Coloration somewhat darker on posterior part of pronotum and venter. Entire body slightly arched longitudinally. Front and hind legs stouter than in female, tibia modified; fore tibia slightly arched, tibial comb about ⅔ as long as tibia; posterior tibia arched, distally with a black pad on inner side for grasping the female in phoresy (Fig. 10). Pregenital abdomen without modifications. Genital segments as shown in Figure 12. Parameres symmetrical, narrow (see Fig. 13). Length, 2.34 mm; width, 0.72 mm.

Macropterous male: Coloration and structural characteristics similar to macropterous female except pronotum not as abruptly narrowed anteriorly (Fig. 4). Length, 2.59 mm.; width, 1.04 mm.

Habitat data. The type locality was a wide unshaded river of shallow depth flowing through a bed of fine sand in the dry deciduous forest country southeast of Morondava. This location was 10 km north of a newly emplaced Amoco oil rig at a site
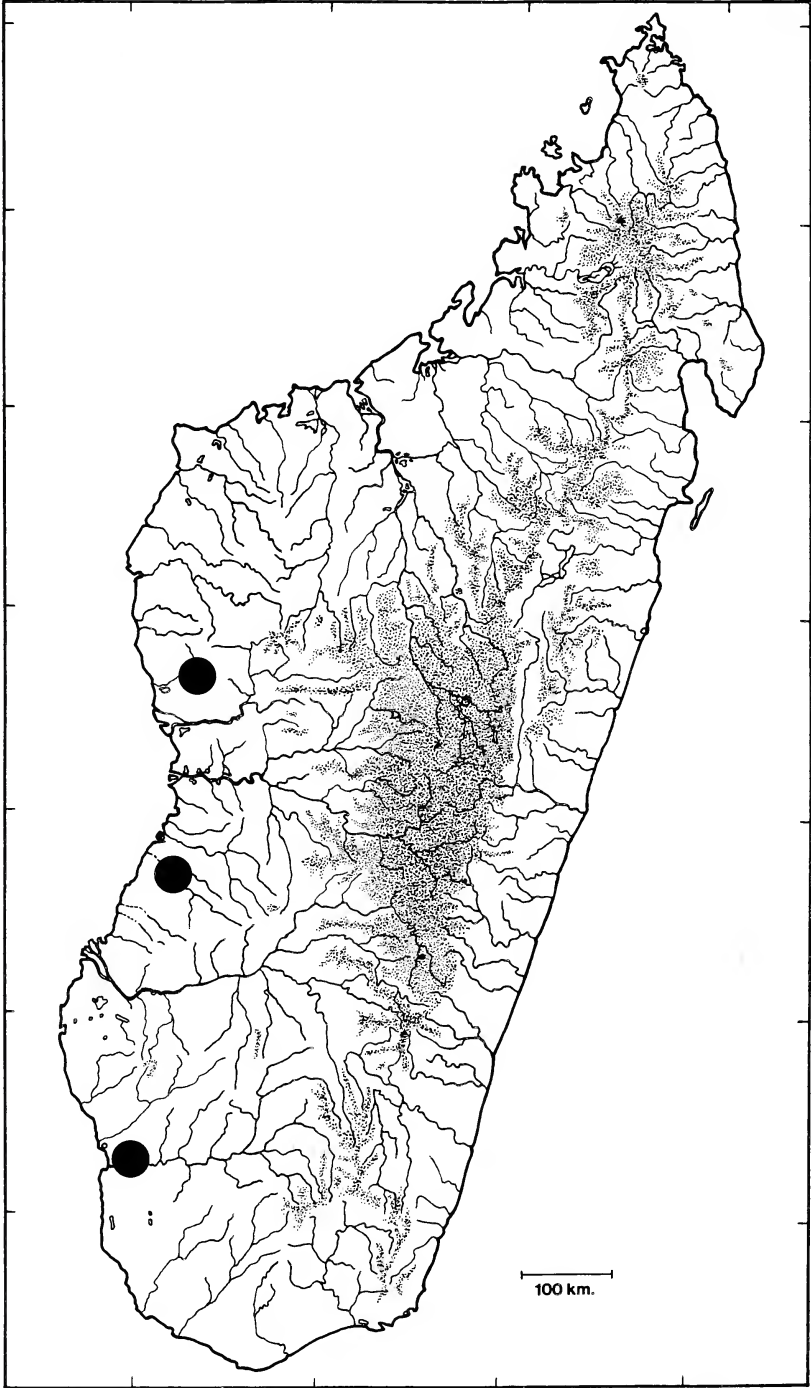
Fig. 14.   Distribution of *Aphrovelia phoretica* in Madagascar. Areas above 1,000 m shaded.

company officials called "Betsimba," and although this name does not appear on any recent maps of Madagascar it is included as a reference point because of the lack of any other nearby villages or landmarks. Specimens of *A. phoretica* were found on rafts of foam that had accumulated in eddies behind fallen logs and other debris caught along the edge of the river channel. At the time of our collecting the rainy season had just commenced and the river was running knee deep and perhaps 30 meters wide. It had obviously been at a much higher flow stage several days prior to our arrival, as was witnessed by the large tangles of debris stranded far up on the banks. Western Madagascar experiences a prolonged dry season for at least half of each year (Donque, 1972), and at this time many of the sandy rivers typical of this region vanish completely. However we were assured by oil company workers and Malagasy locals that this particular stream always kept some small amount of surface flow even in the driest months.

Additional specimens of *A. phoretica* were taken along the Onilahy River, a very large stream draining the Mahalfaly and Horombe plateaus and the Isalo Massif to the south and east of Tulear. This stream was in spate at the time of our collections due to recent upstream rains and thus was considerably larger than the river near Betsimba, running over a kilometer in width and several meters in depth. Here again populations of *Aphrovelia* were found on rafts of foam caught amid debris and overhanging tree branches at the river's edge. This particular locality on the Onilahy was at Sept Lacs, where a spring fed stream originating in the cliffs of the adjoining Mahalfaly Plateau cascades through a series of seven limestone pools to enter the main river. Like the river near Betsimba, this area retains permanent flowing water throughout the dry season.

A single winged male from the Poisson collection is also at hand from "foret Antsingy," literally "forest of the tsingy," near Antsalova. The Malagasy term "tsingy" refers to highly eroded limestone pinnacles in areas of karst terrain, in this case the Bemaraha Plateau. Presumably this specimen came from a perennial spring issuing from the limestone, much like the Sept Lacs locality described above.

Etymology. The name *phoretica* refers to the propensity of the males or nymphs to ride atop the females "piggy-back" (phoresy). This behavior was observed in many pairs in the field, and is manifested in modifications of the male to facilitate phoresy. We have alcohol preserved specimens still locked together that demonstrate this coupling.

Holotype. apterous male, and allotype, apterous female: MADAGASCAR, **Tulear Prov.**, sandy river 10 km N of Betsimba oil drill site, 105 km SE of Morondava, 107 m (350 ft), water temp. 28°C., November 25, 1986, CL 2287, J. T. and D. A. Polhemus (USNM).

Paratypes. MADAGASCAR, **Tulear Prov.**: many males and females, same data as type (JTPC, TSIM); many males and females, Onilahy River at Sept Lacs, 70 km SE of Tulear, 20 m (65 ft), water temp. 28°C., November 30, 1986, CL 2296, J. T. and D. A. Polhemus (JTPC). **Majunga Prov.**: 1 winged male, Andobo, 190 m (623 ft), foret Antsingy det Antsalova, February 1957, P. Griv. (ZMUC).

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FURTHER DATA ON THE ESTABLISHMENT OF
TETYRA BIPUNCTATA (HERRICH-SCHAEFFER)
(HETEROPTERA: SCUTELLERIDAE) IN QUEBEC

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Abstract.—The establishment of *Tetyra bipunctata* (Herrich-Schaeffer) in Québec is reported. Associated plants and overwintering sites of the species are determined for the province.

The previously reported range of *Tetyra bipunctata* (Herrich-Schaeffer), the shield-backed pine seedbug, in northeastern North America included the following state records (McPherson, 1980, 1982): Connecticut, District of Columbia, Indiana, Maryland, Michigan, Minnesota, New Jersey, New York, Ontario, Virginia, Wisconsin. The same author (1982) reported the northern range limit of this distribution to occur from Minnesota east through northern Michigan and southern Ontario, Canada.

Larochelle (1983) reported *T. bipunctata* for the first time in Québec, based on the finding of one overwintering adult female on 8 October 1979 under dead leaves on the floor of a forest of pine and birches in Saint-Lazare-Station (Vaudreuil Co.), a small locality in southwest Québec, south of the Montréal Island. Extensive collecting throughout the province during the summers of 1980–1985 has provided new data on associated plants, distribution, and spread of the species and confirmed its establishment in Québec. These new observations are based on 93 specimens of 2nd to 5th instars and adults collected in three localities in the southern part of the province. Figure 1 shows the actual known distribution of the species in that area.

The label information for all 93 specimens is given below and is accompanied by associated plant data. The abbreviations f., m., ins.2, ins.3, ins.4, ins.5, and ad. refer to the female, the male, the 2nd to 5th instars, and the adult, respectively.

—Gatineau Co.; Parc de la Gatineau; Belvédère Champlain; 1.IX.1985, 1 ins.3, 4 ins.5; *Pinus sylvestris* (Scotch pine).

—Rouville Co.; Mont-Saint-Hilaire; 8.VIII.1985; 1 ins.4; *Pinus sylvestris* (Scotch pine).

—Saint-Maurice Co.; Trois-Rivières; 7.VIII.1982, 2 ins.4; 7.IX.1985, 7 ins.2, 5 ins.3, 9 ins.4, 38 ins.5, 19 ad. (9 f., 10 m.); *Pinus banksiana* (Jack pine).

Specimens are located in the Larivière-Larochelle collection.

Trois-Rivières (Saint-Maurice Co.) constitutes the northernmost distribution point of *T. bipunctata* in North America and an extension of more than 80 miles of its previously known distribution in Québec.

T. bipunctata is generally associated with pine. It has long been described as a "southern species," especially in times when the most northern limit of its range was
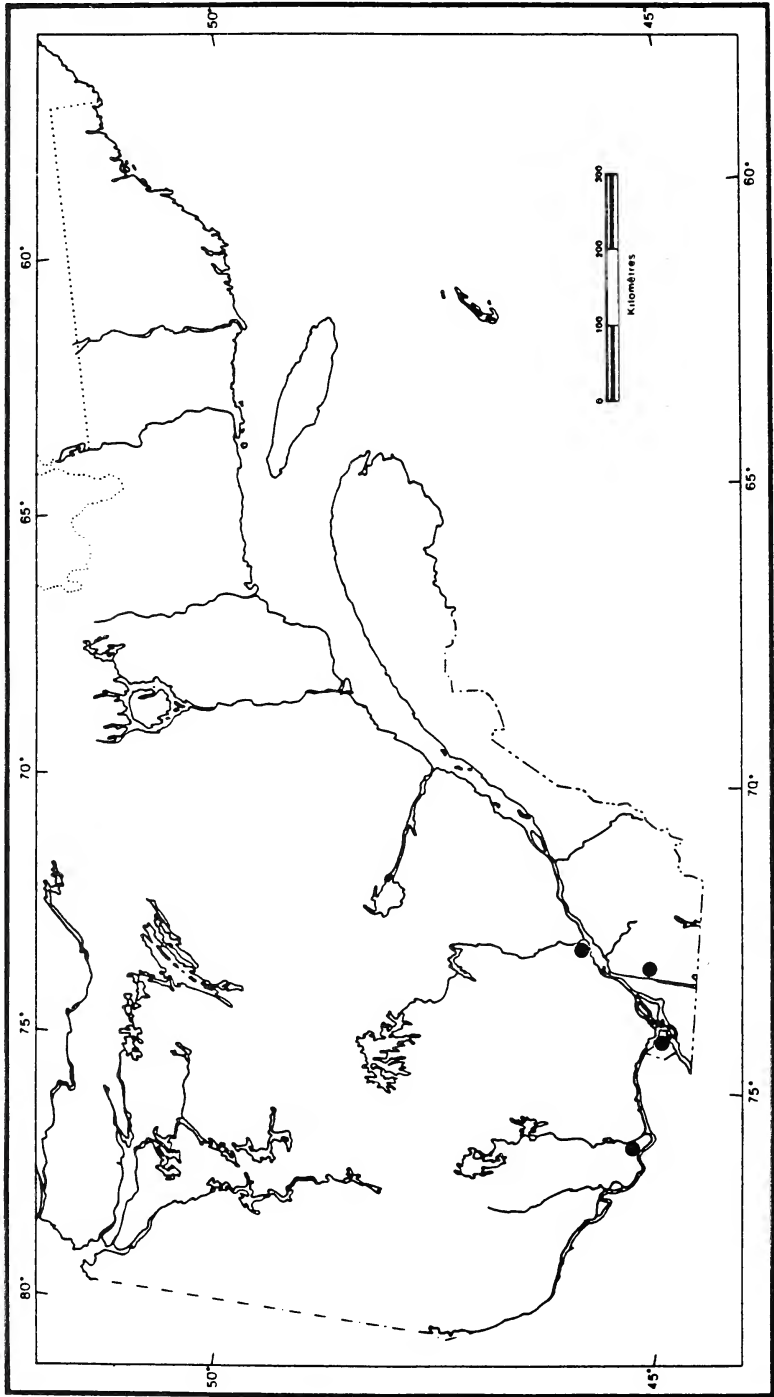
Fig. 1. Distribution of *Tetyra bipunctata* (Herrich-Schaeffer) in Québec.

known from Long Island (Blatchley, 1926) and its association was with southern species of pines. A study conducted in Wisconsin (Gilbert et al., 1967) on the life history of this species, showed its association with northern species of pines as well. Our findings confirm their observations of this scutellerid on *Pinus banksiana*. We also recognize *Pinus sylvestris* as an associated plant in Québec, as the adult and most nymphal stages were found on this tree. The overwintering site and stage (see above) observed in the province agree with those observed in Wisconsin.

The repeated capture of *T. bipunctata* in the same locality and in increasing numbers suggest its successful establishment in the area, although further collection there and in other similar habitats is needed to ascertain that fact. Furthermore, the finding of various life stages of the species indicates its ability to breed in a rigourous climate like that of Québec. We feel that *T. bipunctata* could be found in various locations between the ones already known, as both *Pinus banksiana* and *P. sylvestris* are widespread in the area where they have been commonly planted along highways, in government plantations, and as ornamentals.

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THE GENUS *ABLAPTUS* STÅL
(PENTATOMIDAE: DISCOCEPHALINAE: DISCOCEPHALINI)

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Abstract.—Diagnoses are given for the genus *Ablaptus* Stål and the type species, *A. amazonus* Stål. Two new species, *A. brevirostrum* and *A. tavakiliani,* from Central America and French Guiana, respectively, are added to the previously monotypic genus.

The genus *Ablaptus* Stål is one of 32 genera in the tribe Discocephalini that form the "long-headed group," i.e., discocephalines in which the length of the head is greater than the interocular width. There is no key to the genera of the tribe and no modern treatment of many of the included genera, *Ablaptus* being one such genus. Therefore, diagnoses are given here for the genus and type species. Two new species are added to the previously monotypic genus, one of them from Costa Rica and Panama and the other from French Guiana.

Ablaptus Stål

Ablaptus Stål, 1864:49. Type species: *Ablaptus amazonus* Stål, 1864, by monotypy.

Diagnosis. Length of head about 1.2–1.8 times interocular width. Distance between ocelli about 0.55 of interocular width; distance from each ocellus to nearest eye 0.3–0.4 distance between ocelli. Width of head across eyes 0.6–0.7 basal width of scutellum. Dorsal outline of head before eyes smoothly arcuate, sometimes with slight anteocular concavity (Fig. 2); apices of juga overlapping. Disk of head nearly flat. Antennae each 5-segmented; basal segment nearly reaching apex of head. Bucculae weakly produced anteriorly, more strongly so posteriorly.

Mesial length of pronotum 1.2–1.8 times length of head. Prehumeral disk of pronotum strongly declivent. Scutellum reaching between imaginary parallel lines connecting anterolateral and posterolateral connexival angles of penultimate abdominal segment. Costal angle of each corium lying above last connexival segment. Mesosternum stoutly carinate mesially, lateral halves not tumescent. Metasternum somewhat produced, mesially carinate. Ostiolar ruga on each side extending about 0.75–0.80 distance from mesial limit of ostiole to lateral margin of metapleuron. Ostiole large, crescent shaped, acutely angled mesially. Tarsi 3-segmented.

Sternite 3 (2nd visible) subtuberculate mesially. In male, anterior margins of sternites 6 and 7 projecting cephalad mesially, each forming acute angle, their combined length at meson 0.55–0.70 length of abdominal venter. Tergite 7 of male with mesial process on posterior margin (Figs. 1, 6, 11).

Pygophore extending on each side as long, stout projection set off from remainder of pygophore by suture (Figs. 1, 5, 10); dorsal and ventral pygophoral margins much reduced, genital cup of extracted pygophore entirely visible from dorsal view. Pair

of variously shaped appendages arising from membranous portion of anterior wall of genital cup, one on each side of and adjacent to proctiger.

Comments. The current taxonomic knowledge of discocephalines is so meager that a short diagnosis of *Ablaptus,* sufficient to separate the genus from other described genera of the group, must be accompanied by a caveat as to its infallibility. It appears, however, that *Ablaptus* is distinguished by a combination of subtuberculate third sternite, carinate meso- and metasterna, large ostioles with elongated ostiolar rugae, 3-segmented tarsi, length of basal segment of each antenna (nearly reaching margin of head), lack of anteocular processes and absence of a gibbosity on basal disk of scutellum.

KEY TO MALES OF *ABLAPTUS* SPECIES

1. Ventral margin of pygophore with 3 pairs of processes, middle pair long, digitiform (Fig. 1) .... *amazonus* Stål
–   Ventral margin of pygophore with 1 pair of processes or with none (Figs. 3, 8) 2
2. One pair of processes present on ventral margin of pygophore, these short, acute (Fig. 3) .... *brevirostrum,* n. sp.
–   Ventral margin of pygophore lacking processes (Fig. 8) .... *tavakiliani,* n. sp.

Ablaptus amazonus Stål
Figs. 1, 2

Ablaptus amazonus Stål, 1864:49–50.

Diagnosis. Antennal segment 4 stramineous except for scattering of dark dots basally. Rostrum reaching nearly to middle of abdominal venter; apex of segment 2 attaining mesocoxae, that of segment 3 reaching metacoxae. Metasternal carina slightly arcuate in profile, truncate posteriorly. Mesial process on posterior margin of tergite 7 long, compressed and expanded apically; lateral corners of diamond shaped expansion spinose.

Three pairs of processes present on ventral margin of genital cup; mesial and lateral pairs subtriangular, and between these on each side a long, digitiform process (Fig. 1). Parameres arched, curving ventrad and laterad, each expanded near top of arch, especially on mesial side, to form inverted, irregularly shaped cup. Mesial carina on proctiger subapical, strong, formed by deep impression on each side; apex of proctiger compressed on each side, densely covered by long hairs. Appendage at base of proctiger on each side bent ventrad, densely fringed mesially with long hairs; fringe covering lateral surface of paramere at base.

Measurements (mm). Length of head 2.8, width across eyes 4.05. Length of segments 1–4 of antennae (5th missing) 1.2, 1.7, 1.9, 3.3, —. Length of rostral segments 1–4 about 1.2, 2.6, 1.9, 1.0. Interocular width 2.25; distance between ocelli 1.2, from ocellus to nearest eye 0.5. Width of pronotum across humeri 9.8, mesial length 3.8. Basal width of scutellum 5.6, length 7.3. Ratio of mesial length to lateral length of sternite 5 in male 15:100, of mesial length of sternites 6+7 to mesial length of abdominal venter 68:100. Length of body excluding genitalia 15.5.

Type. The type, which was examined, is conserved in the Naturhistoriska Riksmuseet, Stockholm, Sweden.

Comment. This species is known only from the type.
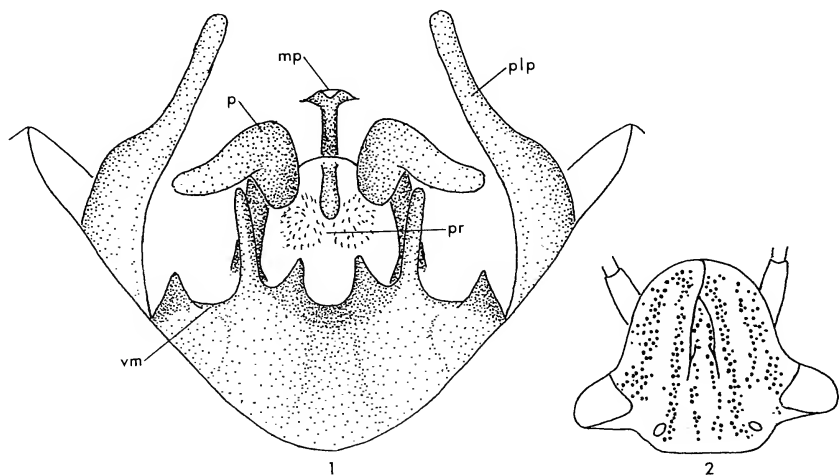
Figs. 1–2. *A. amazonus.* 1. Pygophore, caudoventral view. 2. Head. Symbols: mp, mesial process of tergite 7; p, paramere; plp, posterolateral projection; pr, proctiger; vm, ventral margin.

Ablaptus brevirostrum, new species
Figs. 3–7

Description. Dark stramineous above and below with fuscous punctation and fine, rufous specks dispersed over pronotum, scutellum and hemelytra. Head evenly arcuate before eyes in female, with shallow anteocular concavity in male. Punctures scattered in broad band along lateral margins of juga; irregular, narrow band of punctures running along mesial margin of each jugum and continuing across vertex just mesad of corresponding ocellus; line of punctures on each side of tylus also extending across vertex. Disk of head nearly flat. Basal 3 segments of each antenna thickly dotted with fuscous; narrow subbasal ring on segment 4 and basal ¼ of segment 5 stramineous, remainder of these segments fuscous. Apex of rostrum reaching base of abdomen; segment 2 reaching middle of mesosternum and segment 3 reaching middle of metasternum.

Humeral angles slightly acute, narrowly rounded, each projecting laterad of corresponding hemelytron by about ½ width of eye. Anterolateral margins of pronotum nearly straight with fuscous, submarginal line becoming marginal just before large, polished, stramineous spot on each humerus. Cicatrices not elevated, matte, partially defined by short rows of black punctures. Punctation thickest behind imaginary transhumeral line and arranged there mostly in irregular, transverse lines.

Fovea in each basal angle of scutellum small, black, composed of a few contiguous punctures; margins of scutellar apex slightly reflexed on each side, narrowly bordered with dark macule. Costal margin of each corium narrowly bordered in black basally; punctures irregularly aggregated on endocorium, forming lines and bands on exocorium; junction with membrane sigmoid, costal angle acute and lying above last connexival segment; membrane fumose with 9–11 simple veins. Connexivum increasingly exposed from segment 3 to 7; color and punctation similar to corium; narrow, black border interrupted near posterolateral angle of each segment.
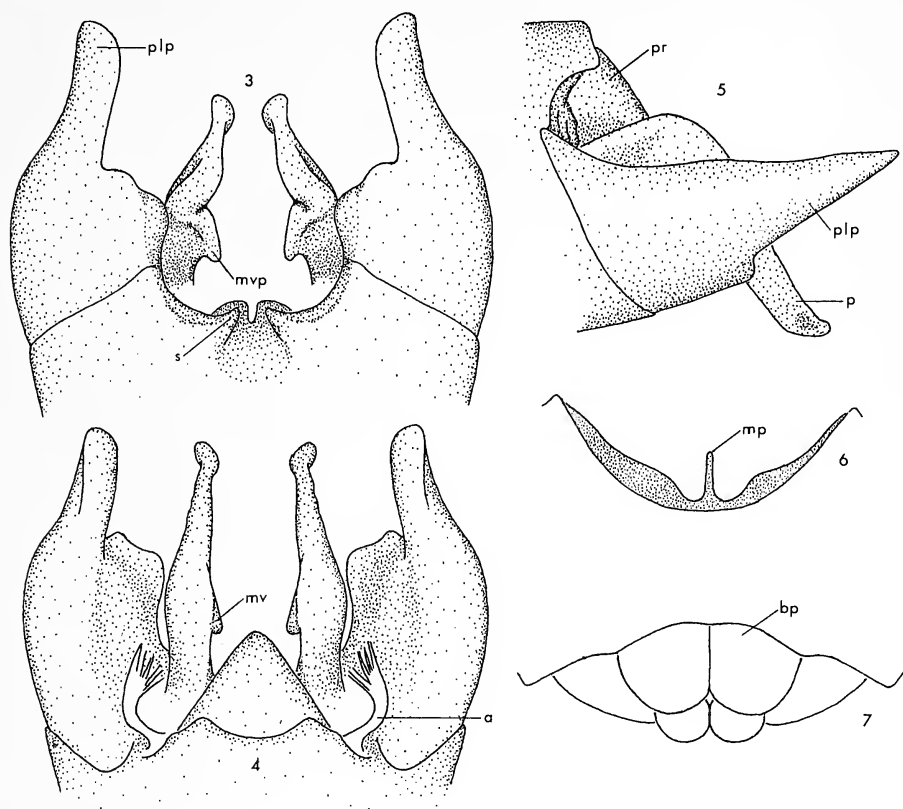
Figs. 3–7. *A. brevirostrum.* 3. Distal portion of pygophore, ventral view (proctiger omitted). 4. Same, dorsal view. 5. Same, lateral view. 6. Posterior margin of tergite 7 (stippled), ventral view with pygophore removed. 7. Genital plates, caudoventral view. Symbols: a, appendage; bp, basal plates; mp, mesial projection; mvp, mesoventral projection of paramere; p, paramere; plp, posterolateral projection; pr, proctiger; s, spine.

Venter rather uniformly and densely punctate. Ostiole large, crescent shaped; ruga thin, weakly produced. Metasternal carina truncate posteriorly. Legs except tarsi thickly stippled with large, discrete, black dots; tarsi and apex of each tibia suffused with crimson on superior surfaces. Spiracles black, oval, those on abdominal segment 2 (first visible) partially or completely exposed. All trichobothria located laterad of imaginary band connecting spiracles on each side and continued to abdominal apex.

Mesial projection on posterior margin of tergite 7 of male spinose, about 0.9 mm long; posterior margin of tergite 7 shallowly concave on each side of projection (Fig. 6). In male, a pair of small, apically convergent spines lie within concavity on ventral border of pygophore (Fig. 3). Posterolateral pygophoral projection on each side narrowing abruptly about ⅖ distance from suture separating projection from remainder of pygophore and apex of projection (Fig. 5). Parameres arched, curving ventrad, slightly retrorse toward apex, each with obtuse basal tooth and larger, obtuse pro-

jection on mesoventral surface where paramere bends ventrad; inferior surface of paramere concave between these projections (Figs. 3, 4). A long, curved appendage bearing tuft of long hairs apically arising on each side at base of proctiger. A blunt, subapical and subventral projection covered with long hairs present on each side of proctiger. In female, only paratergites 8 and 9 and basal plates visible (Fig. 7).

Measurements (mm). Measurements of holotype with those of paratype in paren-thesis. Length of head 2.6 (reflexed and unmeasured in paratype), width across eyes 3.9 (3.7). Length of segments 1–5 of antennae 1.1, 1.9, 1.7, 3.0, 2.8 (1.0, 1.9, 1.9, —, —). Length of rostral segments 1–4 about 1.3, 2.2, 1.7, 1.0 (1.1, 2.0, 1.6, 1.0). Interocular width 2.1 (2.3); distance between ocelli 1.2 (1.2), from ocellus to nearest eye 0.4 (0.5). Width of pronotum across humeri 10.4 (9.9), mesial length 4.3 (4.1). Basal width of scutellum 6.1 (5.9), length 7.5 (7.1). Ratio of mesial length to lateral length of sternite 5 in male 25:100, of mesial length of sternites 6+7 to mesial length of abdominal venter 62:100. Length of body excluding genitalia 15.3 (15.4).

Types. Holotype, male labeled (a) "Turrialba, C. R., 20 VI '48, F. Schrader, 583" and (b) (red label) "*Ablaptus brevirostrus* H. Ruckes, HOLOTYPE." Paratype, female labeled (a) "B. C. I. Panama, 29 V '57, F. Schrader, A118" and (b) (red label) "*Ablaptus brevirostrus* H. Ruckes, ALLOTYPE." Both specimens are deposited in the American Museum of Natural History.

Comments. During the course of his work on discocephalines, the late Professor Herbert Ruckes recognized several new taxa, which he left undescribed. As indicated by the labeling of the type series, this species is one of those taxa.

Schrader (1960) included this species, misidentified for him as *A. amazonus,* in a cytological study of the "harlequin lobe" found in the testis of many pentatomid species.

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Ablaptus tavakiliani, new species
Figs. 8–11

</div>

Description. Similar in appearance to *A. amazonus* but differing as follows. An-tennal segment 3 dotted with fuscous on basal half, a few fuscous dots at base of segment 4, segments 3 to 5 otherwise immaculate. Rostrum reaching anterior margin of sternite 4 (3rd visible); apex of segment 2 reaching mesocoxae. Short, fuscous mark on anterolateral pronotal margin just before each humeral angle, another on posterolateral margin, the two marks separated. Humeri punctate, without large, polished spot at each humeral angle. Black, mesial macule present on basal disk of scutellum; margins of scutellar apex not reflexed, lacking macules. Connexiva little exposed. Endocorium of each hemelytron heavily suffused with rufous.

Most punctures on venter rufous. Lateral half of each side of abdominal venter finely and very densely dotted with rufous.

In male, mesial projection on posterior margin of tergite 7 digitiform (Fig. 11). Ventral pygophoral surface mesially concave distally, the concavity black distally and with a dark castaneous, oval spot on each side near base of posterolateral py-gophoral projection; each projection with step-like depression basally on mesial mar-gin (Fig. 8); mesodorsal surface of each projection concave with teardrop shaped excavation (Fig. 9). Each paramere expanded laterad and ventrad subapically, forming flattened, approximately triangular superior surface and cusped mesial surface with
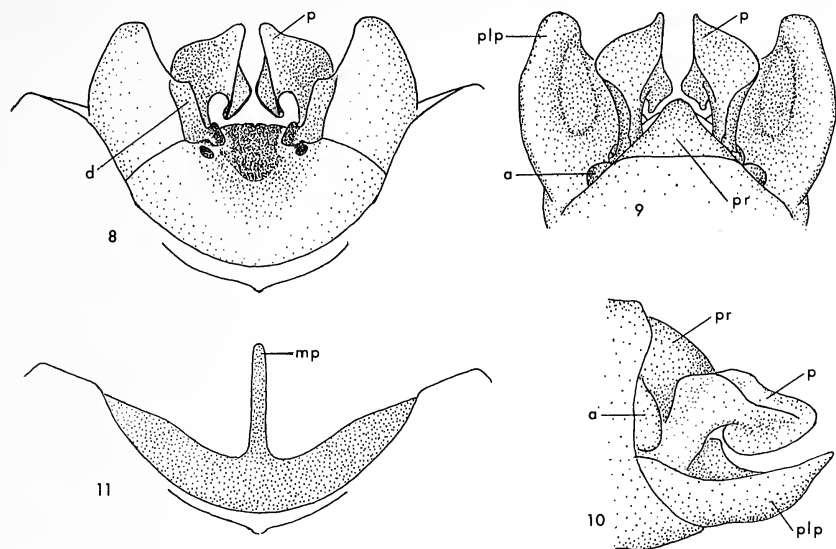
Figs. 8–11. *A. tavakiliani.* 8. Pygophore, ventral view. 9. Distal portion of pygophore, dorsal view. 10. Same, dorsolateral view. 11. Posterior margin of tergite 7 (stippled), ventral view with pygophore removed. Symbols: a, appendage; d, depression in posterolateral projection; mp, mesial projection; p, paramere; plp, posterolateral projection; pr, proctiger.

arcuate ventral margin (Figs. 8, 9, 10). Proctiger conical from dorsal view. Appendage arising on each side of genital cup (from membranous anterior wall) compressed, posteriorly arcuate, appearing as conspicuous plate from dorsolateral view (Fig. 10).

Measurements (mm). Length of head 2.50, width across eyes 3.45. Length of segments 1–5 of antennae 0.9, 1.4, 1.5, 2.4, 2.4. Length of rostral segments 1–4 about 1.1, 2.0, 1.4, 0.8. Interocular width 1.8; distance between ocelli 1.0, from ocellus to nearest eye 0.35. Width of pronotum across humeri 7.8, mesial length 3.0. Basal width of scutellum 4.9, length 5.7. Ratio of mesial length to lateral length of sternite 5 in male 35:100, of mesial length of sternites 6+7 to mesial length of abdominal venter 54:100. Length of body, excluding genitalia 11.5.

Type. Holotype, male, from French Guiana, labeled "Roura, 23.VII.1981. G. Tavakilian, Collection O.R.S.T.O.M." Illegible symbols precede the date on the label. Deposited in the Museum National d'Histoire Naturelle, Paris.

Comments. This species is named for the collector, Gerard Tavakilian.

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THE GENUS *MATHIOLUS* DISTANT
(HEMIPTERA: PENTATOMIDAE)

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Abstract.—The genus *Mathiolus* Distant, 1889, is transferred from the pentatomid subfamily Discocephalinae to the nominate tribe of the Pentatominae. A diagnosis is given for the genus. The type species is redescribed and a lectotype designated. Two new species are added to the genus, *M. labiatus* from Venezuela and *M. tumidus* from Ecuador.

Distant (1889) proposed *Mathiolus generatus* as a new genus and new species in the Discocephalinae based on specimens collected by Champion in Guatemala. Since then, neither the genus nor species has been mentioned in the literature, except in the catalogs of Lethierry and Severin (1893) and Kirkaldy (1909). Here the genus is redefined and the type species redescribed. Two new species are described, one from Venezuela and the other from Ecuador.

In pentatomids of the subfamily Discocephalinae, the first rostral segment projects posteriorly beyond the bucculae and usually reaches well onto the prosternum. In all genera of Discocephalini and most genera of Ochlerini, the two tribes of Discocephalinae, the labium originates behind an imaginary plane perpendicular to the longitudinal axis of the body and at the anterior limit of the eyes. Females in all genera of Ochlerini, and males of some genera, have the superior surface of the first tarsal segment of each hind leg excavated or flattened. In *Mathiolus,* the basal segment of the rostrum lies entirely between the bucculae, the labium originates in front of the eyes, and the superior surface of the first tarsal segment of all legs of both sexes is convex. *Mathiolus* is therefore removed from the Discocephalinae and placed in the nominate tribe of the Pentatominae among those genera without a spine or tubercle at the base of the abdominal venter.

Mathiolus Distant, 1889

Mathiolus Distant, 1889:326; Lethierry and Severin, 1893:87; Kirkaldy, 1909:218.

Diagnosis. Each hind and middle femur armed subapically on inferior surface with single tubercle or spine; all tibiae broadly sulcate; tarsi 3-segmented. Base of abdominal venter subtuberculate mesially; all pairs of trichobothria laterad of imaginary band connecting spiracles on each side. Ostiolar rugae lanceolate, each extending approximately ¼ distance from mesial limit of ostiole to lateral margin of metapleuron. Prosternum with obtuse carina on each side running obliquely from anterior pronotal margin to juncture between procoxae; both mesosternum and metasternum carinate mesially.

Females or both sexes brachypterous; membrane lacking veins, wrinkled, present but much reduced in brachypterous forms; claval suture obscure. Scutellum about

$\frac{1}{10}$ longer than wide at base. Anterior margin of pronotum shallowly and rather evenly concave; anterolateral margins nearly straight, narrowly reflexed. Juga convergent or contiguous before tylus. Antennae 5-segmented; segments 1 and 2 subequal in length; segments 3 and 4 also subequal in length, each as long or somewhat longer than segments 1 and 2 combined. Basal segment of rostrum lying entirely between bucculae; latter evanescent near base of head, each rounded anteriorly, without tooth.

Type species. Mathiolus generatus Distant, 1889, by monotypy.

Comments. Several western hemisphere genera in Pentatomini have some femora armed, but only Mathiolus has a single, preapical tubercle or spine on each of the hind and middle femora.

KEY TO *MATHIOLUS* SPECIES

1. Juga greatly swollen apically along mesial margin; 2nd rostral segment just surpassing procoxae .... *tumidus,* new species
   – Anterior disk of head approximately level; 2nd rostral segment reaching mesocoxae   2
2. Inferior surface of each hind femur with preapical spine (Fig. 15); spiracles round .. .. *labiatus,* new species
   – Inferior surface of each hind femur with obtuse tubercle (Fig. 9); spiracles oval .... *generatus* Distant

Mathiolus generatus Distant, 1889
Figs. 1–9

Mathiolus generatus Distant, 1889:326, Pl. 31 figs. 4, 5; Lethierry and Severin, 1893: 87; Kirkaldy, 1909:218.

Redescription. General color dark brown with black punctation; sterna, precoxae, legs, metapleura except evaporative areas, costal margins of hemelytra ventrally, rostrum and segments 1–4 of antennae stramineous, all except rostrum with dark punctures or dots; abdominal venter dark castaneous.

Juga contiguous before tylus, anteocular margins slightly produced (Fig. 3). Ocelli small, scarcely larger than largest nearby punctures. A few short setae present on eyes. Basal segment of each antenna reaching apex of head. Second rostral segment reaching but not surpassing mesocoxae. Pronotum moderately convex transversely, more so anteriorly than posteriorly, scarcely declined toward head. Scutellar disk weakly convex along basal margin; lateral margins nearly straight, distal end of frena indistinct; scutellar apex narrowly rounded; black fovea present in each basal angle. R+M vein weakly defined, with small, pale macule at distal end. In male, junction of membrane and corium of each hemelytron straight, diagonal, with posterolateral angle of corium over last abdominal tergite; posterolateral part of 4th, most of 5th, all of 6th and 7th connexival segments and lateral border of last 2 abdominal tergites exposed; membrane not extending beyond apex of abdomen (Fig. 2). Female brachypterous; all of 7th tergite, nearly all of 6th, and posterolateral corners of 5th exposed; posterolateral margin of each corium broadly rounded; membrane extending onto basal portion of 6th tergite (Fig. 1).

Mesosternum slightly tectiform; metasternum tectiform, moderately produced, arcuate in profile, subtruncate posteriorly. Evaporative area on each metapleuron raised, dark, matte, weakly punctate and furrowed (Fig. 8). Each hind femur with
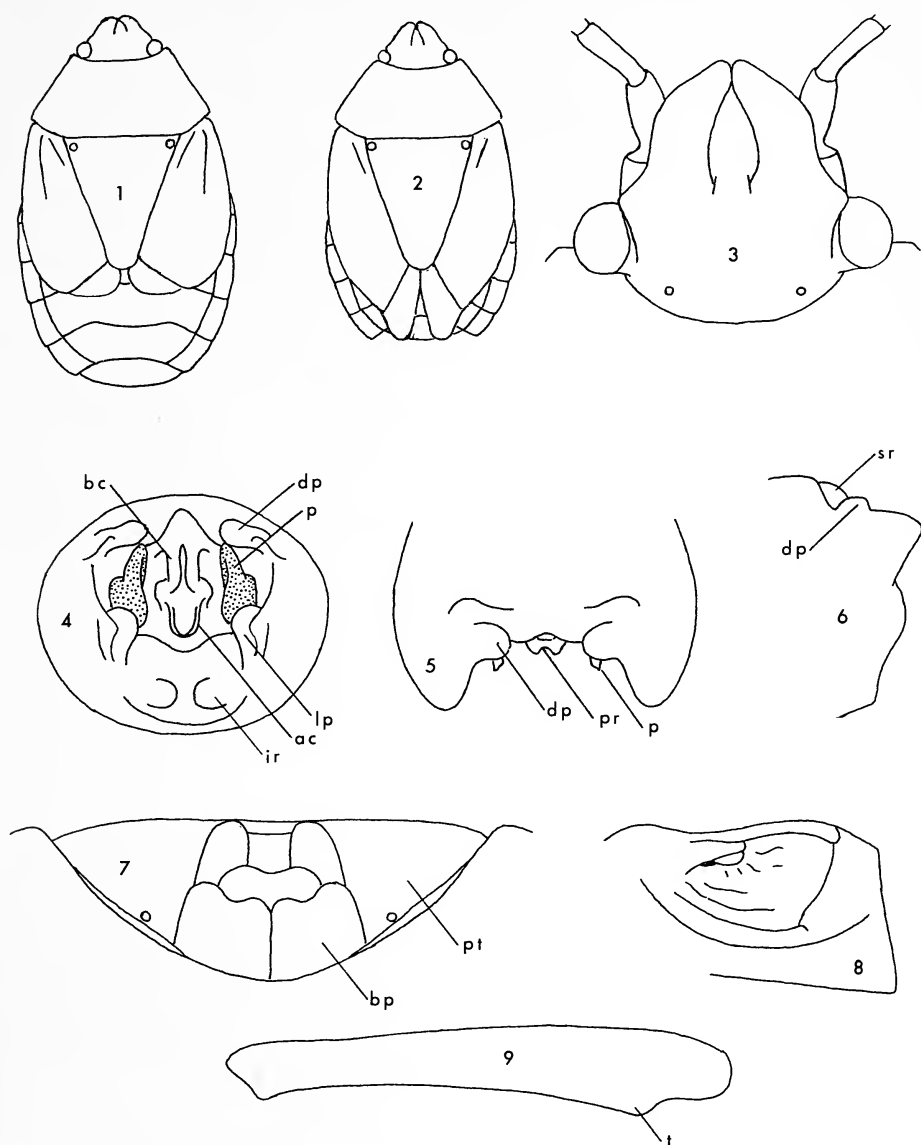
Figs. 1–9. *Mathiolus generatus.* 1. Dorsum, female. 2. Dorsum, male. 3. Head. 4. Pygophore, caudal view. 5. Pygophore, dorsal view. 6. Pygophore, lateral view. 7. Genital plates, caudo-ventral view. 8. Metapleuron. 9. Anterior surface of right hind femur. Symbols: ac, apical carina on proctiger; bc, basal carina on proctiger; bp, basal plate; dp, dorsobasal projection; ir, inferior ridge; lp, lateral projection; p, parameres; pr, proctiger; pt, 8th paratergite; sr, superior ridge; t, tubercle.

low, broad, preapical tubercle on inferior surface (Fig. 9); middle femora less distinctly tuberculate. Spiracles black, oval. Disk of abdominal venter finely punctate laterally, aciculate mesially. Pseudosutures inconspicuous.

Inferior ridge of pygophore with pair of shallow concavities near ventral margin (Fig. 4). Rim of genital cup on each side at dorsal limit of inferior ridge produced mesad as obtuse, lateral projection; dorsolateral portion of rim on each side produced strongly caudad, with stout, obtuse, dorsobasal projection directed mesad (Figs. 4–6). Proctiger with parallel, longitudinal pair of carinae basally and thin pair apically on each side of concavity (Fig. 4).

Spiracle present on each 8th paratergite. Posterior margin of basal plate emarginate, posterolateral angle projecting caudad farther than posteromesial angle (Fig. 7).

Measurements (mm). Head 2.2–2.4 wide, 1.7–2.0 long; interocular width 1.45–1.60; distance between ocelli 0.80–0.90, across ocelli 0.95–1.10, from ocellus to nearest eye 0.30–0.35. Length of segments 1–4 of each antenna 0.50–0.65, 0.45–0.50, 1.20–1.30, 1.15–1.20 (5th missing). Length of rostral segments 2–4 (1 specimen only) 1.40, 1.05, 0.85. Pronotal width 4.4–4.8, mesial length 1.9–2.0. Width of scutellum at base 2.8–3.0, width at distal end of frena 1.3, length 3.5–3.8. Body length 8.9–10.2, width at 4th abdominal segment 5.2–6.0.

Type. The syntypes consist of 1♀, 2♂♂ preserved in the British Museum (Natural History). The following specimen is designated lectotype: ♂, pinned, with pygophore mounted on point, labeled (a) "Cerro Zunil, 4–5000 ft, Champion" (b) "Distant Coll. 1911–383". Paralectotypes are: ♂ carded and labeled (a) "Type" (red-edged circle) (b) "Cerro Zunil, 4000 ft., Champion" (c) "Mathiolus generatus"; 1♀ pinned (re-mounted) and labeled (a) "Cerro Zunil, 4000 ft., Champion" (b) "BCA Hem. I, Mathiolus generatus." In addition, all specimens are labeled "syntype" (blue-edged circle). Distant did not designate type specimens and consequently the "type" label has no validity. The specimen bearing this label is probably the male illustrated in the original description. It was not selected as lectotype, however, because it is less suitable as a reference specimen than the specimen chosen.

Distribution. Known only from the type series collected on Cerro Zunil, Guatemala.

Mathiolus labiatus, new species
Figs. 10–15

Description. General color dark brown with black punctation; precoxae, costal margins of hemelytra ventrally and appendages stramineous; apical halves of last antennal segments fuscous; thoracic pleura mottled stramineous and brown.

Juga projecting a little beyond tylus, convergent but not contiguous apically; anteocular margins slightly produced (Fig. 10). Ocelli obscure in male, small in female but appreciably larger in diameter than any nearby puncture. A few short setae present on eyes. Basal segment of each antenna reaching apex of head in male, exceeding apex of head by diameter of segment in female. Second rostral segment reaching mesocoxae. Pronotum and scutellum similar to *generatus* but scutellar apex more broadly rounded. R+M vein weakly defined except at base, with pale spot at distal end. Both sexes brachypterous, leaving posterolateral part of 5th tergite and all of 6th and 7th tergites exposed; part of 4th connexival segment and all of 5th–7th connexival segments exposed; posterolateral corner of each corium rounded.

Sterna as in *generatus* except metasternum less produced. Evaporative areas raised,
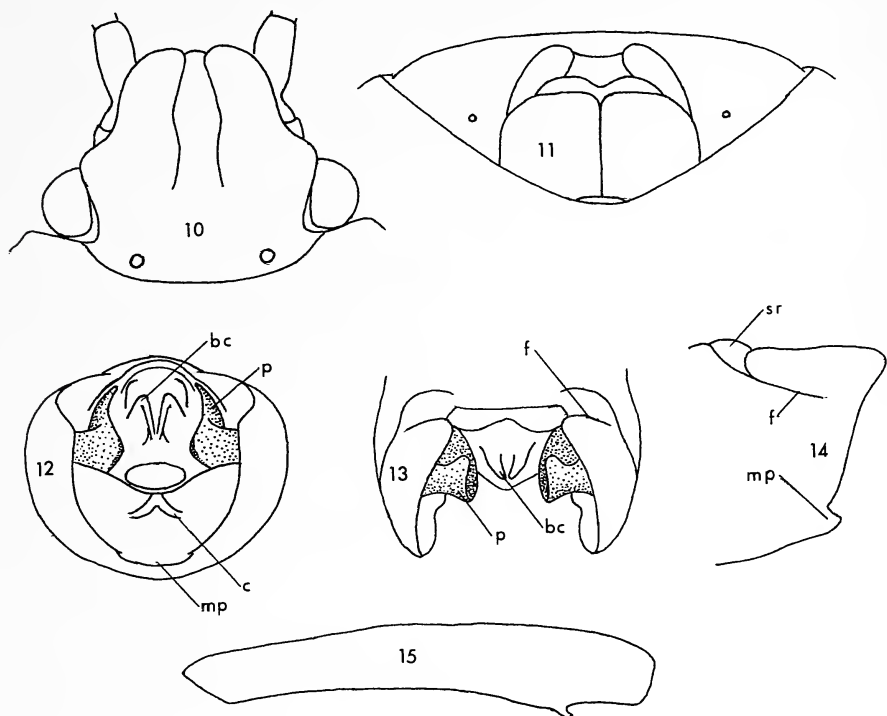
Figs. 10–15. *Mathiolus labiatus*. 10. Head, female. 11. Genital plates. 12. Pygophore, caudal view. 13. Pygophore, dorsal view. 14. Pygophore, lateral view. 15. Anterior surface of right hind femur. Symbols: bc, basal carina of proctiger; c, carina on inferior ridge; f, furrow; mp, mesial projection; p, paramere; sr, superior ridge.

matte, strongly furrowed, punctation black. Each hind and middle femur with short, black preapical spine on low tubercle on inferior surface (Fig. 15). Spiracles black, oval. Disk of abdominal venter finely and rather evenly punctate, aciculate medially.

Inferior ridge of pygophore with chevron-shaped, mesial carina at dorsal margin (Fig. 12). Short, broad, labiate, mesial projection located on ventral rim of genital cup (Figs. 12, 14). Lateral portion of genital cup rim strongly produced, black, divided into dorsolateral and ventrolateral parts by obtuse, external ridge; dorsolateral part separated from remainder of pygophore by furrow (Figs. 13, 14). Parameres cultrate apically, curving dorsad, each with stout plate projecting at right angles from lateral surface. Proctiger with pair of longitudinal, subparallel carinae subbasally; apex slightly concave.

Spiracles on 8th paratergites of female. Posterior margin of basal plates evenly convex from caudoventral view (Fig. 11).

Measurements (mm). Head 1.95–2.05 wide, 1.35–1.55 long; interocular width 1.30–1.40; distance between ocelli 0.75, across ocelli 0.95, from ocellus to nearest eye 0.30 (ocellar measurements of female). Length of segments 1–5 of each antenna 0.50, 0.40–0.45, 0.95–1.05, 0.90–1.00, 1.25–1.30. Length of segments 1–4 of rostrum 0.75–

0.80, 1.35, 0.9–1.05, 0.75–0.80. Pronotal width 4.3–4.8, mesial length 1.6–1.8. Width of scutellum at base 2.6–3.0, length 2.9–3.3. Body length 8.3–9.4, width at 4th abdominal segment 4.8–4.9. The smaller measurement, where a range is given, is that of the male holotype.

Types. Holotype, ♂, labeled (a) "LaGrita, 2400 m. Edo. Táchira, VENEZ. Bordón, leg. 16 III 1983" (b) "Colección del Instituto de Biologia, UNAM, Mexico, D.F." Deposited in the Instituto de Biologia, Universidad Nacional Autónoma de Mexico. Paratype, ♀, labeled same as holotype. Deposited in author's collection.

Distribution. Western Venezuela.

Mathiolus tumidus, new species

Description. Pronotum fuscous, remainder of dorsum dark brown. Venter except metathorax predominately black or fuscous; metathorax, precoxae, costal margins of hemelytra ventrally, and some interstices on abdominal disk stramineous; evaporative areas and metapleura with dark dots surrounding punctures; appendages stramineous, all but rostrum with dark dots, many dots on middle and hind femora and tibiae fusing into small macules. Punctation black.

Juga convergent, strongly tumescent apically along mesial margin. Anteocular margins slightly produced (Fig. 16). Ocelli small but larger in diameter than any nearby puncture. Eyes not setose. Basal antennal segments in male not exceeding apex of head. Second rostral segment just surpassing procoxae; apex of terminal segment lying between metacoxae. Middle third of anterior pronotal margin raised as thin collar; from this a thin, mesial carina extends to vague, transverse, rugose fascia which includes the poorly defined cicatrices; pronotal disk behind fascia rugosely punctate. Scutellum only slightly convex, rugosely punctate, with black fovea in each basal angle; postfrenal portion well defined, apex moderately rounded. Claval suture of each hemelytron obscure; R + M vein well developed with a small, ivory spot at distal end; male brachypterous (female unknown), leaving all of 7th tergite, posterior part of 6th (all of it laterally) and posterolateral corners of 5th exposed; remnant of membrane present; posterolateral corner of each corium broadly rounded.

Sterna as in *generatus* excepting metasternum less arcuate in profile. Evaporative areas raised, matte, inconspicuously furrowed, with irregular black punctation. Hind and middle femora each with short, black, preapical spine on inferior surface (Fig. 17). Spiracles black, round; a small, irregular, subcalloused, stramineous macule contiguous with and mesad of each spiracle. Abdominal disk sparsely aciculate and obscurely punctate mesially, densely punctate laterally.

Inferior ridge of pygophore large, with low, irregularly shaped prominence along mesial part of dorsal margin (Fig. 19). Dorsolateral portion of genital cup rim strongly produced, fuscous, set apart dorsally from remainder of pygophore by furrow (Figs. 18, 20); between this portion of genital cup rim on each side and superior ridge, a small, rugose, cushion-shaped tumescence present on anterior wall of genital cup; dorsolateral corners of pygophore appearing notched from caudal view (Fig. 19). Parameres truncate distally, both dorsal and ventral apical margins broadly rounded; stout plate on lateral surface of each paramere curved slightly ventrad. Proctiger strongly crested mesially.

Measurements (mm). Head 2.05 wide, 1.55 long; interocular width 1.35; distance between ocelli 0.75, across ocelli 0.95, from ocellus to nearest eye 0.30. Length of antennal segments 1–4 (5th missing) 0.50, 0.40, 0.90, 0.90. Length of segments 1–4
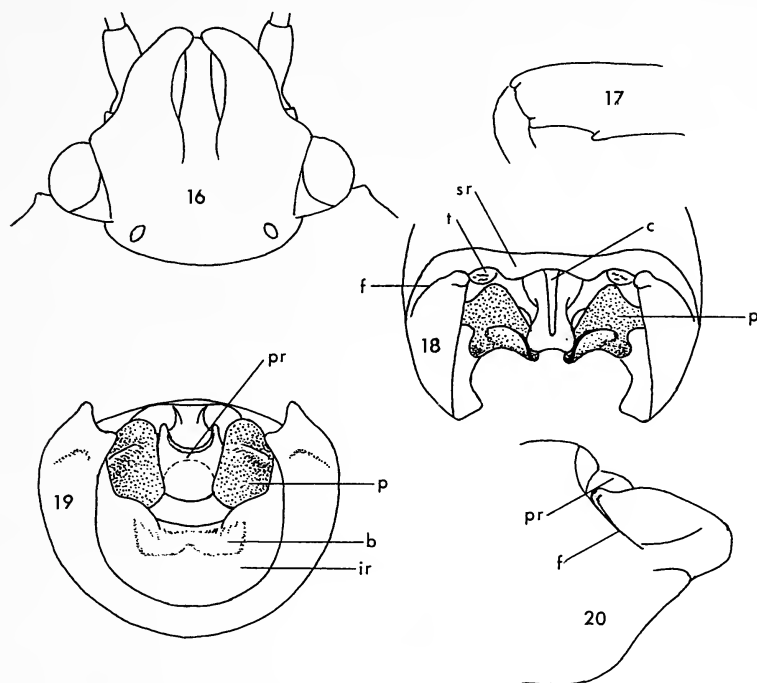
Figs. 16–20. *Mathiolus tumidus.* 16. Head. 17. Anterior surface of right hind femur. 18. Pygophore, dorsal view. 19. Pygophore, caudal view. 20. Pygopore, lateral view. Symbols: b, prominence on inferior ridge; c, carina on proctiger; f, furrow; ir, inferior ridge; p, paramere; pr, proctiger; sr, superior ridge; t, cushion-shaped tumescence.

of rostrum 0.60, 1.10, 0.85, 0.70. Pronotal width 4.6, mesial length 1.7. Width of scutellum at base 2.8, at distal end of frena 1.9; length 3.0. Body length 8.0, width at 4th abdominal segment 5.1.

Type. Holotype, ♂ labeled "Ecuador: Napo, Reventador" and "on Solanum umbellatum." Deposited in the Instituto de Biologia, Universidad Nacional Autónoma de Mexico. No paratypes.

Distribution. Eastern Ecuador.

ACKNOWLEDGMENTS

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SPINALANX, A NEW GENUS AND TWO NEW SPECIES OF PENTATOMINI FROM SOUTH AMERICA (HEMIPTERA: PENTATOMIDAE)

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Abstract. — The genus *Spinalanx* and two included species, *S. monstrablis* and *S. corusca,* are described as new from South America. The genus is one of six genera of Pentatomini in the western hemisphere that do not have a median spine or tubercle at the base of the abdominal venter but do have the inferior surfaces, at least, of some or all femora armed. A key is provided for the separation of these genera.

Among the genera of Pentatomini that are characterized by the absence of a median spine or tubercle at the base of the abdominal venter, there are six in the western hemisphere that have at least the inferior surface of some or all pairs of femora armed. These six genera, one of them new, may be separated by the following key.

KEY TO GENERA

1. Ostiolar ruga on each side reaching about ¾ distance from mesial limit of ostiole to lateral margin of metapleuron .... *Seneticus* Rolston
– Ostiolar ruga on each side reaching about ³⁄₁₀ distance from mesial limit of ostiole to lateral margin of metapleuron 2
2(1). Only middle and hind femora armed, each bearing a single, preapical spine or tubercle on inferior surface (Fig. 1); females or both sexes brachypterous .... *Mathiolus* Distant
– Front femora, at least, variously armed on inferior surface with one or more pairs of large, preapical spines or tubercles, or with numerous, small, seta-bearing tubercles (Figs. 2, 3); hemelytra well developed 3
3(2). Width of scutellum at distal end of frena about ⅔ or less of basal width; spines or tubercles on inferior femoral surfaces differing greatly in size, those nearest apices of femora largest (Fig. 2) 4
– Width of scutellum at distal end of frena about ½ or more of basal width; at least inferior femoral surfaces armed with many, small, seta-bearing tubercles of approximately equal size (Fig. 3) 5
4(3). Interocular width ½ width of head across eyes; rostrum reaching mesocoxae .... *Sibaria* Stål
– Interocular width ⅗ width of head across eyes; rostrum reaching metacoxae .... *Ladeaschistus* Rolston
5(3). Each corium with impunctate bands paralleling R+M vein and clavical suture; posterior margins of basal plates entire, smooth .... *Agroecus* Dallas
– All of each corium punctate; posterior margins of basal plates tuberculate .... *Spinalanx*, new genus

Spinalanx, new genus

Type species. Spinalanx monstrablis, new species.

Diagnosis. Third abdominal (second visible) sternite without mesial spine or tu-
bercle. Ostiolar rugae auriculate. Femora armed with numerous, small, seta-bearing
tubercles scattered on all but posterior surfaces. Width of scutellum at distal end of
frena about ⅗ of basal width. Each corium entirely punctate, without impunctate
bands along veins and clavical suture. Anterolateral margins of pronotum denticulate
(Figs. 4, 12). Area between posterior margin of pygophore and inferior ridge broad,
nearly flat, unexcavated (Fig. 6). Basal plates irregularly convex but not tumid, their
posterior margins tuberculate (Figs. 8, 9, 13, 14).

Description. Broadly ovate; slightly convex dorsally, strongly so ventrally. Dorsal
surface of head moderately convex transversely; tylus slightly longer than juga. First
of 5 segments in each antenna nearly reaching apex of head. Anterolateral margins
of pronotum concave in dorsal view, denticulate (Figs. 4, 12). Scutellum broadly
rounded apically, about ⅗ as wide at distal end of frena as at base. All of each corium
punctate, without impunctate bands along veins or clavical suture; hemelytral mem-
branes fumose, with parallel venation. First rostral segment protruding little or not
at all beyond bucculae, second segment reaching mesocoxae or nearly so, fourth
segment extending to or slightly past metacoxae. Prosternum flat, mesosternum mod-
erately carinate mesially, metasternum weakly concave. Ostiolar rugae auriculate;
evaporative areas relatively small. Each femur armed on all but posterior surface
with numerous, small, scattered, seta-bearing tubercles (Fig. 3). Tibiae sulcate. Tarsi
3-segmented. Third abdominal sternite without mesial spine or tubercle. Mesial
trichobothrium of each pair lying within imaginary, curved band connecting spiracles
on each side of abdomen.

Area between posterior margin of pygophore and inferior ridge unexcavated, form-
ing nearly flat border (Fig. 6). Membranous pad present on each lateral wall of genital
cup. Parameres without basal cup (Fig. 7). Thecal appendages present (Fig. 11). Basal
plates weakly convex, their posterior margins tuberculate (Figs. 8, 9, 13, 14).

Comments. This genus appears to be related most closely to *Agroecus* Dallas, from
which it differs conspicuously in having rather uniformly punctate coria, weakly
convex basal plates that are tuberculate along the posterior margins, membranous
pads on the lateral walls of the genital cup, and parameres without a pronounced
basal cup.

Spinalanx monstrablis, new species
Figs. 3–11

Description. Dorsum dark brown to fuscous, becoming fuscous to black along
anterolateral pronotal borders and on humeri; apices of humeral angles sometimes
pale. Dorsal punctation dense, strong, black, slightly weaker and closer on head,
anterior pronotal margin and humeri than elsewhere; many punctures on scutellum
arranged in short, irregular, transverse lines; interstices on pronotal and scutellar
disks unevenly rugose, some subtuberculate or subcarinate, especially on pronotum.
Jugal margins subparallel for middle third of distance from eyes to apex of head;
anteocular margins weakly convex; tylus projecting slightly beyond juga. Antennae
light to dark brown, basal fourth of each terminal segment pale. Anterolateral pronotal
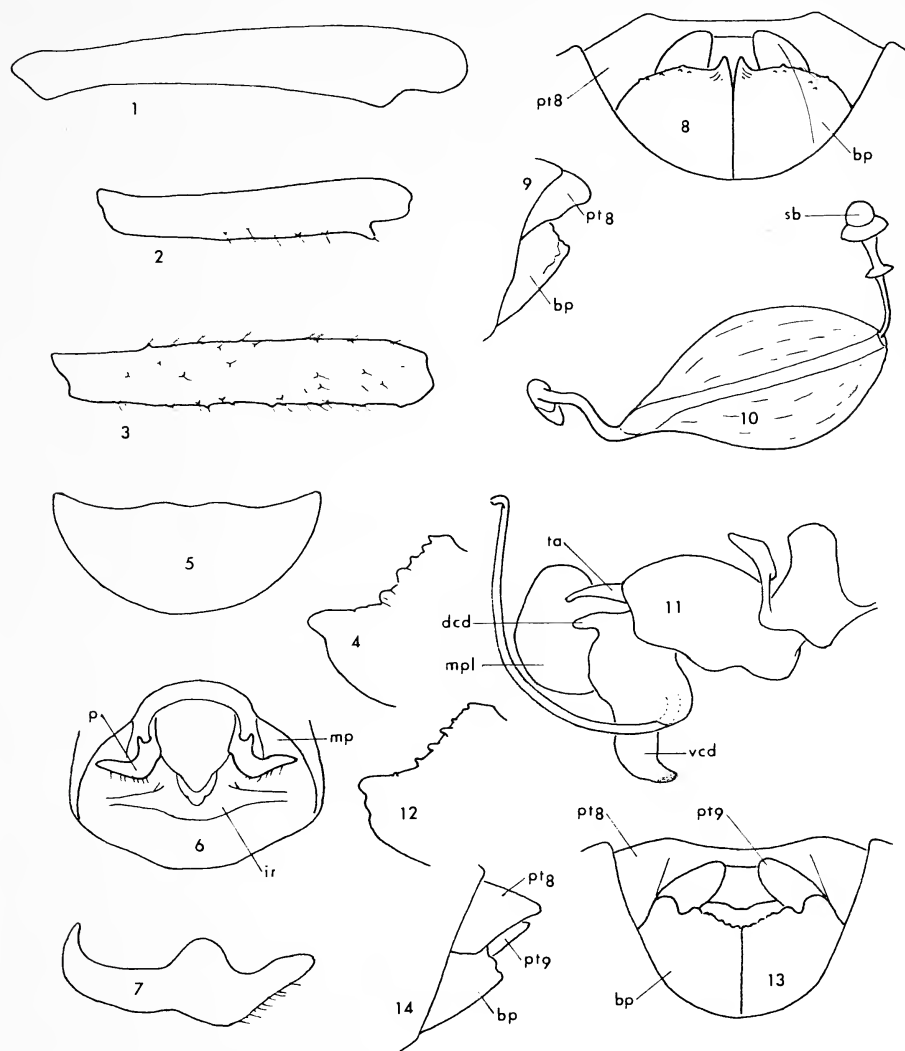
Figs. 1–14. 1–3. Front femur, anterior view. 1. *Mathiolus generatus* Distant. 2. *Ladeaschistus armipes* (Stål). 3. *Spinalanx monstrablis*. 3–11. *Spinalanx monstrablis*. 3. Femur. 4. Humerus and anterolateral pronotal margin. 5. Pygophore, caudal view. 6. Genital cup. 7. Paramere. 8. Genital plates, caudoventral view. 9. Genital plates, lateral view. 10. Spermatheca. 11. Theca and related structures. 12–14. *Spinalanx corusca*. 12. Humerus and anterolateral pronotal margin. 13. Genital plates, caudoventral view. 14. Genital plates, lateral view. Symbols: bp, basal plate; dcd, dorsolateral conjunctival diverticulum; ir, inferior ridge; mp, membranous pad; mpl, median penial lobe; p, paramere; pt8, paratergite 8; pt9, paratergite 9; sb, spermathecal bulb; ta, thecal appendage; vcd, ventrolateral conjunctival diverticulum.

margins concave in dorsal view, each with 5–8 stout denticles; humeral angles produced laterad, narrowly rounded; margin immediately caudad of each humeral angle concave (Fig. 4). Scutellum slightly wider at base than long.

Connexiva narrowly exposed, serrate; posterolateral angle of each segment and sometimes a marginal macule pale. Posterior margin of each corium diagonal, nearly straight between rounded mesial angle and costal margin; costal angle nearly right angular, lying above posterior half of penultimate segment of connexivum, sometimes reaching last connexival segment.

Venter light brown to yellowish brown. Punctation fuscous to black, rather dense and uniform. Evaporative areas with small, fuscous punctures. Spiracular peritremes fuscous. Legs concolorous with venter; numerous large, dark spots and macules scattered on femora and tibiae.

Broad, shallow depression in each basal plate paralleling posterior margin of last sternite; posterior margin concavely emarginate just laterad of acute posteromesial angle (Fig. 8); tubercles present on posterior margin and border laterad of emargination. Spermathecal bulb spheroid (Fig. 10).

Posterior margin of pygophore slightly sinuous from both caudal and caudoventral view (Fig. 5); pygophoral surface broadly and weakly carinate mesially. Parameres digitiform distally, expanded dorsally just distad of point of articulation (Fig. 7). Conjunctiva with dorsolateral pair and ventrolateral pair of diverticula (Fig. 11) median penial lobes laminar, large.

Measurements (mm, holotype in parentheses): Length from apex of head to apex of abdomen 8.04–9.30 (8.04). Length of head from apex to posterior margin of ocelli 1.99–2.26 (1.99), width across eyes 2.17–2.43 (2.17). Length of segments 1–5 of each antenna 0.52–0.61, 0.84–0.90, 0.92–1.13, 1.12–1.25, 1.21–1.40 (0.55, 0.88, 0.92, 1.14, 1.29). Length of segments 2–4 of rostrum 1.73–1.88, 0.59–0.77, 0.63–0.70 (1.88, 0.63, 0.63). Mesial length of pronotum 1.91–2.21 (1.91), width at humeri 5.36–6.15 (5.36). Scutellar length 3.13–3.75 (3.13), basal width 3.25–3.94 (3.39), width at distal end of frena 1.66–2.47 (2.10).

Types. Holotype: ♂ labeled "COLOMBIA: Putomayo: Sta. Rosa de Sucumbios, Kofan Indian Village, Rio San Miguel, 400 m. Sept. 5–9, 1971. B. Malkin"; deposited in American Museum of Natural History. Paratypes: 8♂♂, 7♀♀; labeled same as holotype (4♂♂, 2♀♀ AMNH); "COLOMBIA: Putumayo: Santa Rosa, Kofan Indian Village, Headwaters Rio S. Miguel, Oct. 2–15, 1970. P. Burchard, B. Malkin" (1♀, LHR); "Rio Negro near Villavicencio, Nov. 1, 1965. COLOMBIA, E. W. Schmidt-Mumm" (1♀ AMNH; 1♂, 1♀ DAR); "PERU: Dpto. Loreto, Quebrada Orán ca 5 km N Rio Amazonas, 85 km NE Iquitos, el. 110 m. VI-1984, L. J. Barkley" (1♂ LHR); "PERU, Loreto, Estiron. Rio Ampiyacu, XI-13 to XII-9, 1961. B. Malkin leg" and "night sweeping along forest trail" (1♂, 1♀ AMNH); "PERU, Loreto, Headwaters Rio Loreto-Yacu, Yucua Indian Vill. April 21–May 1, 1970. B. Malkin" (1♂ AMNH); "ECUADOR, Pompeya on Napo R. 40 km from Coca, Nape-Pastaza Prov. 1965" and "L. E. Peña Collector" (1♀ AMNH).

Spinalanx corusca, new species
Figs. 12–14

Description. Dorsum without magnification brunneus with disperse, fine glitter of reflected light; dorsum with magnification light castaneous becoming dark castaneous

along anterolateral pronotal borders and on humeri, and luteous on post-frenal portion of scutellum. Dorsal punctation dense, strong, regular, somewhat weaker and denser on head, anterior pronotal margin, humeri, toward scutellar apex and on coria; punctures rufous to dark castaneous verging to fuscous on tylus, vertex of head and basal disk of scutellum; many punctures on basal disk of scutellum confluent and arrayed in short, irregular, transverse lines; interstices on pronotum and basal portion of scutellum rugose; a pair of small, ivory tubercles located at posterior margins of cicatrices near their mesial limits. Jugal margins subparallel for middle third of distance between eyes and apex of head; anteocular margins weakly convex; tylus protruding slightly past juga. Pronotal surface weakly depressed around cicatrices, these separated by somewhat elevated triangle with basal angles at the pair of ivory tubercles and apex near anterior pronotal margin; anterolateral pronotal margins concave, each with 6–8 major denticles with ivory apices; humeral angles produced, narrowly round; margin between each humeral angle and hemelytron nearly straight, irregular (Fig. 12). Basal width and length of scutellum equal. Connexiva moderately exposed, serrate; broad, fuscous, lateral borders interrupted on apical 2 or 3 segments. Hemelytra as in *monstrablis* except costal margins weakly crenulate basally.

Venter luteous, abundantly mottled with rufous. Punctation castaneous to fuscous, rather dense and uniform, but tending to aggregations on base of abdomen; punctures on evaporative areas small, deep, fuscous. Spiracular peritremes dark. Legs light tan, becoming dark brown apically on front and middle tibiae, with numerous, large, dark brown macules on femora and tibiae.

Basal plates shallowly and irregularly depressed along proximal border; posterior margin of each plate notched near posterolateral angle, tuberculate between notch and obtuse posteromesial angle (Fig. 13).

Measurements (mm): Length from apex of head to apex of abdomen 8.67. Length of head from apex to posterior margin of ocelli 2.24, width across eyes 2.32. Length of segments 1–5 of each antennae 0.59, 0.81, 0.99, 1.03, 1.25. Length of segments 2–4 of rostrum 1.84, 0.59, 0.59. Mesial length of pronotum 1.95, width at humeri 5.83. Scutellar length and basal width equal, 3.68; width at distal end of frena 2.31.

Type. Holotype: ♀ labeled "Palmer, Prov., Chapere, Dep. Cochabamba, Bolivia, 1000 M. Franz Steinbach, Coll. 1956"; deposited in U.S. National Museum of Natural History. No paratypes.

Comments. This species differs markedly from the type species in the shape of the basal plates. Apparently it differs also in color, shape of the humeri and proportions of the scutellum.

FIRST SOUTHEASTERN U.S. RECORDS OF THE WESTERN HETEROPTERANS *PRIONOSOMA PODOPIOIDES* (PENTATOMIDAE) AND *AUFEIUS IMPRESSICOLLIS* (RHOPALIDAE), WITH A REVIEW OF DISTRIBUTION AND HOST PLANTS

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Abstract.—Two heteropteran species native to western North America, the pentatomid *Prionosoma podopioides* Uhler and the rhopalid *Aufeius impressicollis* Stål, are recorded for the first time from southeastern United States. Populations of *P. podopioides* are reported from northern South Carolina on bracted plantain, *Plantago aristata* Michx., documenting the suspected host relationship for this species; *A. impressicollis* is reported from the same area on Palmer amaranth, *Amaranthus palmeri* S. Wats. Hosts of both heteropterans are native western plants naturalized in the Southeast.

In analyzing postglacial dispersal in certain animal groups, biogeographers have identified relict eastern populations of formerly more widespread western species, including a few coreids among the Heteroptera (Baranowski and Slater, 1986). But in much more recent time (the past one hundred years) several heteropterans indigenous to the western United States have expanded their ranges to include eastern North America. A well-documented example is *Catorhintha mendica* Stål, a Great Plains coreid that has followed the establishment of wild four o'clock, *Mirabilis nyctaginea* (Michx.) Mac Mill. (Nyctaginaceae), along railroad right of ways. Seed contaminating surplus grain products spilled from freight cars, allowing the plant to become naturalized in the East and this specialist herbivore to track its host to eastern Pennsylvania (Balduf, 1957) and eventually to Long Island, New York (Hoebeke and Wheeler, 1982) and Connecticut (Slater, 1983). Spread of the boxelder bug, *Boisea trivittata* (Say), also is well documented. This presumed southwestern rhopalid that develops mainly on boxelder, *Acer negundo* L. (Aceraceae), is now established essentially throughout the eastern states and in southern Ontario (Slater and Schaefer, 1963; Schaefer, 1975). Its spread is believed to have been aided by the extensive planting of boxelder trees east of the original range. Another coreoid, the grass-feeding alydid *Esperanza texana* Barber, is thought to have moved eastward from Texas into the Southeast in recent years (Froeschner, 1980; Wheeler and Henry, 1984).

In 1987, field work in northern South Carolina provided the first southeastern U.S. records of *Prionosoma podopioides* Uhler (Pentatomidae) and *Aufeius impressicollis* Stål (Rhopalidae). Bracted plantain, *Plantago aristata* Michx. (Plantaginaceae), is given here as the first documented host of *P. podopioides*. *Aufeius impressicollis* is reported from Palmer amaranth, *Amaranthus palmeri* S. Wats. (Amaranthaceae), verifying that amaranths are its principal hosts. Previous records of these heteropterans east of the Mississippi River and their host plant relationships are reviewed. Voucher specimens have been deposited in the insect collections of Cornell Univer-

sity, Pennsylvania Department of Agriculture, and U.S. National Museum of Natural History.

Prionosoma podopioides

Distribution. Uhler (1863) described this pentatomid from California; *P. villosum* Provancher, described from British Columbia, and *Neurohalys bucculatus* Bliven, also described from California, are considered junior synonyms of *P. podopioides* (Van Duzee, 1904; Rolston and McDonald, 1984). Van Duzee (1904) noted that this "western species" also is known from Colorado, Nevada, Utah, and south through Arizona and New Mexico to Mexico. Blatchley (1926) did not include this stink bug in his manual of eastern Heteroptera (species occurring east of the 90th meridian); Stoner (1916, 1920) had published records from Iowa and Missouri just west of the 90th meridian. Stoner (1920) gave *P. podopioides* as an example of the tendency of western Heteroptera to spread eastward "where favorable environmental conditions may occur." Records from southern Michigan (McPherson, 1970) and Illinois (McPherson and Cuda, 1975; McPherson, 1982) have remained the easternmost for *P. podopioides* (Fig. 1).

On 9 May 1987, I collected an adult at Pageland (Chesterfield Co.), South Carolina, by sweeping an old field dominated by grasses; weeds, mainly *Rumex acetosella* L. (Polygonaceae); and eastern prickly pear, *Opuntia humifusa* Raf. (Cactaceae). The collection area, a transition zone between the Piedmont Plateau and Coastal Plain, is characterized by white sandy soil. Sweeping the supposed host of this pentatomid, *Plantago aristata,* growing near the original collection site yielded another adult on 3 July 1987, and 12 adults and nymphs (instars III–V) were taken on heads of bracted plantain at a nearby site (4 miles west of Pageland). On 4 July, 7 adults and instars II–V were swept from *P. aristata* along Rt. 151, 0.5 mi north of McBee (Chesterfield Co.) in the Carolina Sandhills. Large numbers were present near Pageland and McBee (many more specimens could have been collected), but this species was not encountered in other areas of Chesterfield Co. or in nearby Anson and Union counties of North Carolina, even though bracted plantain was present along roadsides and in fields.

Host plants. In New Mexico, Ruckes (1937) reported *P. podopioides* as abundant in axils and flowers of a wild sunflower, but the literature strongly suggested that bracted plantain would prove to be a preferred food plant. Froeschner (1941) recorded this "scarce" pentatomid from four counties in Missouri during July, August, September, and December, noting that all but the winter record were from "fields or open woods where the Large Bracted Plantain, *Plantago aristata,* was common." The first Illinois record resulted from its collection near a colony of the same plant. The single female collected was kept alive on heads of *P. aristata* for 1½ months in the laboratory, though no eggs were deposited. Because additional trips to the same site failed to yield more specimens, nothing further could be added to the biology of this "rare" and "poorly known species" (McPherson and Cuda, 1975).

Discovery of large populations on bracted plantain at two localities in South Carolina substantiates this plant as a primary host of *P. podopioides.* I also collected 4 fifth-instar nymphs on this plant 7 mi west of Conway (Faulkner Co.), Arkansas, on 12 June 1987; this is a new state record (see Barton and Lee, 1981). The nymphs completed their development on inflorescences and seed heads of *P. aristata.*
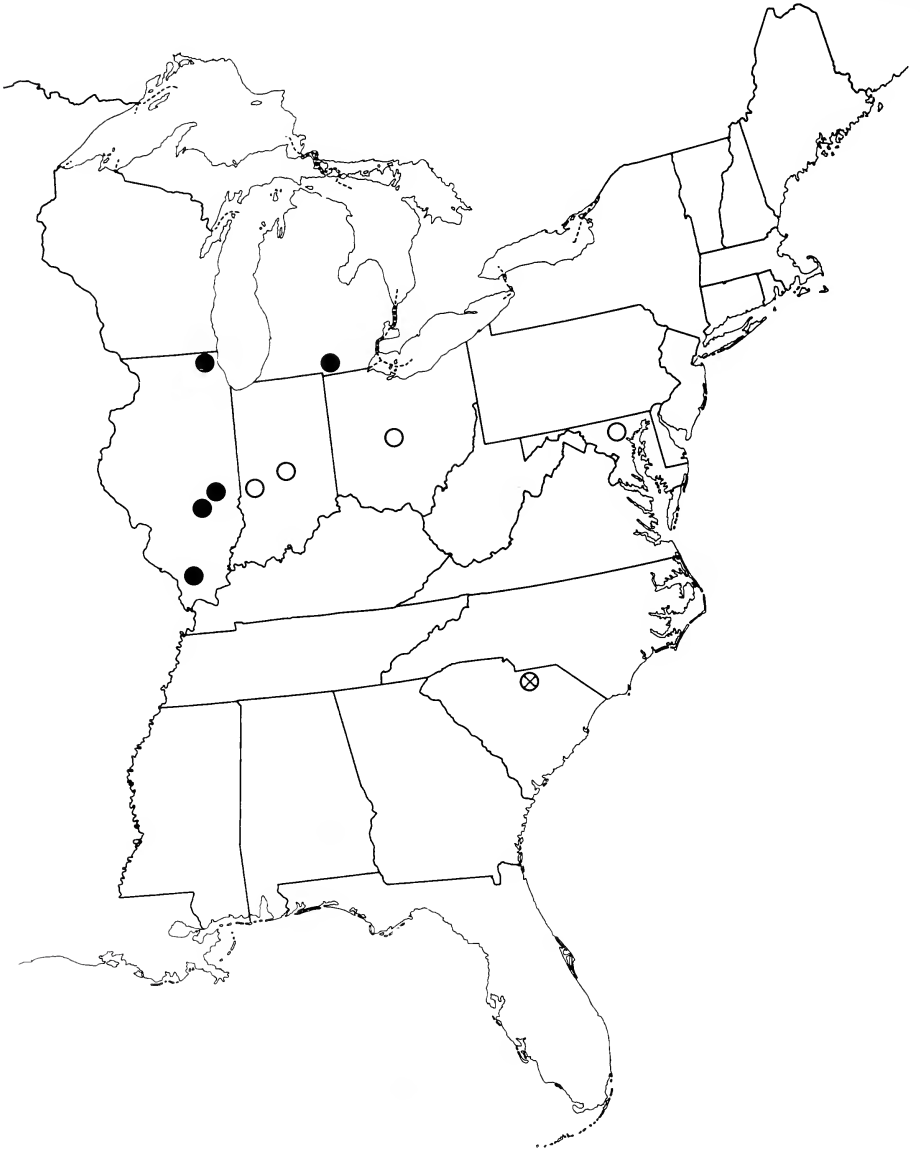
Fig. 1.   Previously published records of *Prionosoma podopioides* (closed circles) and *Aufeius impressicollis* (open circles) east of the Mississippi River (see text for references) and new localities for both species (× in circle).

Gray (1886) remarked that bracted plantain is most abundant west of the Missis-sippi. Nearly a century later, Muenscher (1980) still referred to *P. aristata* as most common in the "middle western United States, where it is native." This plant, however, is widely naturalized in the eastern states, having begun its spread in the late 1860's (Fernald, 1950).

Aufeius impressicollis

Distribution. Of probable Sonoran origin (Slater, 1974), this rhopalid is widely distributed in the western United States, ranging from Iowa, Missouri, Nebraska, and South Dakota west to Idaho and Washington, and south from California to Texas; it also is known from Mexico and Guatemala (Wheeler, 1984). Few records are available east of the Mississippi (Fig. 1). Osborn and Drake (1915) reported *A. impressicollis* from Columbus, Ohio, which remained the easternmost record until Wheeler (1984) recorded it from Baltimore, Maryland. This species also has been collected in Indiana (Blatchley, 1926).

I swept 2 adults at Pageland, South Carolina, on 9 May 1987 near the old field where *Prionosoma podopioides* had been collected. No additional specimens were found at this site on 3–4 July, but *Amaranthus* spp., the apparent principal hosts (Wheeler, 1984), could not be located. But further south in Chesterfield Co., along Rt. 151, 8.5 mi north of McBee, large numbers of adults were encountered (17 were collected) on inflorescences of *Amaranthus palmeri* growing at the edge of a cultivated field. A population of the rhopalid estimated at several hundred (19 adults were collected) was found on the same host growing in a crop field along Rt. 1, 2 mi northeast of McBee in the sandhills region. On 4 September adults were less numerous at the field northeast of McBee. A mating pair was observed on an inflorescence and single adults were collected on heads of two other *A. palmeri* plants.

Host plants. Wheeler (1984) reviewed ecological data available in the scant liter-ature on this rhopalid and from labels attached to museum specimens, noting that records suggested a preference for amaranthaceous plants and possibly Chenopodi-aceae. After finding adults on smooth pigweed, *Amaranthus hybridus* L., at Baltimore, he was able to obtain oviposition in the laboratory and to rear the bugs from egg to adult on this plant. That *A. impressicollis* specializes on amaranths is now supported by its collection on Palmer amaranth in South Carolina and on *Amaranthus* spp. in Nebraska in July 1986 (Wheeler, unpubl.).

The host plant in South Carolina, Palmer amaranth, is native to the southwestern states and is a common weed in Texas (Muenscher, 1980). *Amaranthus palmeri* has spread into the Mississippi Delta states and apparently is generally distributed north to most of Missouri, southern Illinois and Indiana, nearly all of Kentucky, extreme southern West Virginia, and the southern half of Virginia (Elmore et al., 1986). Gleason and Cronquist (1963) listed it as an occasional weed occurring at scattered stations in the Northeast.

DISCUSSION

Available evidence suggests that the discovery of *Prionosoma podopioides* and *Aufeius impressicollis* in the Southeast should not be attributed to relict eastern populations or to accidental introduction with commerce. Instead, the South Carolina

populations seem to be the result of recent range expansions. These heteropterans, indigenous to western North America, appear to have spread eastward following establishment of their host plants east of their original ranges. The plants may have become established in parts of the southeastern United States as early as the mid-to-late nineteenth century, but there is no evidence to suggest how long the bugs have been established. Because the heteropteran fauna of this region has not been thoroughly collected and collectors could overlook these noneconomic species, *P. podopioides* and *A. impressicollis* could have been present in the Southeast for several decades.

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PSEUDOXENETUS REGALIS
(HETEROPTERA: MIRIDAE: ORTHOTYLINAE):
SEASONAL HISTORY AND DESCRIPTION OF FIFTH INSTAR

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Abstract.—The seasonal history of the mirid *Pseudoxenetus regalis* (Uhler) was followed on white oak, *Quercus alba* L., in central Missouri during 1984–1986. This univoltine species is a specialist feeding only on oaks. Overwintering eggs hatched in early April; adults first appeared in early May and are present until the end of May. Notes are given on the North American distribution, polymorphism, and host plants. The fifth-instar nymph is described and illustrated.

Pseudoxenetus regalis (Uhler) is widely distributed in eastern North America (Carvalho, 1958) and one of many plant bugs restricted to feeding on oaks, *Quercus* spp. Despite this wide distribution, virtually nothing is known regarding the biology of this species. Two color morphs exist and were initially described as separate species by Uhler (1890). The morph "*scutellatus*" usually has a black pronotum and white scutellum and "*regalis*" usually has an orange pronotum and white scutellum. Henry (1985) concluded that *regalis* and *scutellatus* were conspecific and placed *regalis* as the senior synonym of *scutellatus*.

Herein I outline the seasonal history of *P. regalis* based on samples collected in Missouri during 1984–1986, discuss the distribution, polymorphism, and the host plants of this species, as well as describe and illustrate the fifth instar nymph.

STUDY SITE AND METHODS

The study site in Columbia (Boone Co.), Missouri, was an open field dominated by large white oak, *Quercus alba* L., and shagbark hickory, *Carya ovata* (Mill.) K. Koch, with an understory of closely mowed grasses and forbs, surrounded by a mature oak-hickory woodland border.

I sampled weekly from early May to mid-June 1984. In 1985-1986, sampling began in late March to determine earliest eclosion and thereafter collections were made every 3–4 days until adults were no longer collected (early June). Mirids were sampled by sweeping branches with a standard 15-inch beating net. All specimens taken during ca. 20 minutes of sampling were captured. The number taken was small, with a typical sample consisting of only 4–10 specimens. Immatures were placed in alcohol and sorted to instar in the laboratory; adults were killed using ethyl acetate, mounted, labeled, and deposited, with the immatures, as voucher specimens in the Wilbur R. Enns Entomology Museum (EMUM), University of Missouri–Columbia.

To determine oviposition sites, adults were caged on twigs of white oak in the laboratory and any oviposition noted.

RESULTS AND DISCUSSION

Seasonal history (Fig. 1). Hatching of overwintering eggs occurred shortly after the leaves began to unfold, approximately 14 April in 1985 and 9 April in 1986. Early instars (1st–2nd) were observed feeding on the staminate flowers and expanding leaves. Early instars are whitish green, closely resembling the color of the flowers and young foliage. Subsequent instars (3rd–5th) are red to reddish brown and easily observed feeding on the staminate flowers and foliage. The population consisted of second instars by mid-April and third and fourth instars by late April. In both 1985 and 1986 fifth instars were first collected on 29 April. Adults were first collected on 3 May in 1985 and 1 May in 1986, and were present for only 3–4 weeks both years. Adults last appeared in the weekly collections on 30 May in 1985 and 13 May in 1986. Three females were collected on 7 June in 1984. The latest known collection of *regalis* in Missouri is 24 June (Blinn and Yonke, 1985).

In the laboratory a female deposited a single egg 3.5 mm below one of next year's lateral leaf buds. The egg was placed perpendicular to the stem just beneath the surface of the stem.

Geographic distribution and polymorphism. Figure 2, compiled from the literature and specimens examined in the Wilbur R. Enns Entomology Museum, shows the North American distribution of each color morph for *regalis*. In general, *regalis* is widely distributed east of the 100th meridian. Both color morphs can be found throughout its distribution; however, there is a gradation from north to south with the "*scutellatus*" morph more common in the North and the "*regalis*" morph more common in the South (Henry, 1985).

Froeschner (1949) noted that *regalis* was less common than *scutellatus* in Missouri. Of 130 Missouri specimens examined, 17% fit the "*regalis*" morph and 83% the "*scutellatus*" morph. Considerable color variation exists in this species. Several "*scutellatus*" morphs have the scutellum fuscous to black rather than the typical ivory white. One specimen examined from Liberty Co., Florida, fits the typical "*scutellatus*" morph except the scutellum is orange.

Nymphs apparently do not show the color variation that characterizes the adults. The description of the fifth instar below is based on specimens obtained from the study population in which 8% of the adults collected fit the "*regalis*" morph and 92% fit the "*scutellatus*" morph.

Host plants. Pseudoxenetus regalis is a specialist feeding only on oaks. Froeschner (1949) stated that *regalis* was common on the foliage of oaks in open woods. Specimens examined in the Wilbur R. Enns Entomology Museum have been taken on *Quercus alba, Q. imbricaria* Michx., *Q. rubra* L., *Q. stellata* Wang. and *Q. velutina* Lam. Additional host records include *Q. marilandrica* Muenchh., *Q. prinoides* Willd. (=*muhlenbergii*), and *Q. virginiana* Mill. (Knight, 1941).

In addition to oaks, adults have been recorded from apple, *Pyrus malus* L., and ash, *Fraxinus* sp. (Knight, 1941). I have examined a specimen collected on hickory, *Carya* sp., at Columbia, Missouri (EMUM). These are not true hosts and should be considered adventitious records.

Description of fifth instar (N = 5) (Fig. 3). Length 4.50–5.35 mm; elongate, somewhat formicoid, uniformly, sparsely clothed with erect, pale setae. Head: width across eyes 0.87 mm, vertex 0.52 mm, frons and vertex reddish brown, gula red. Rostrum: length
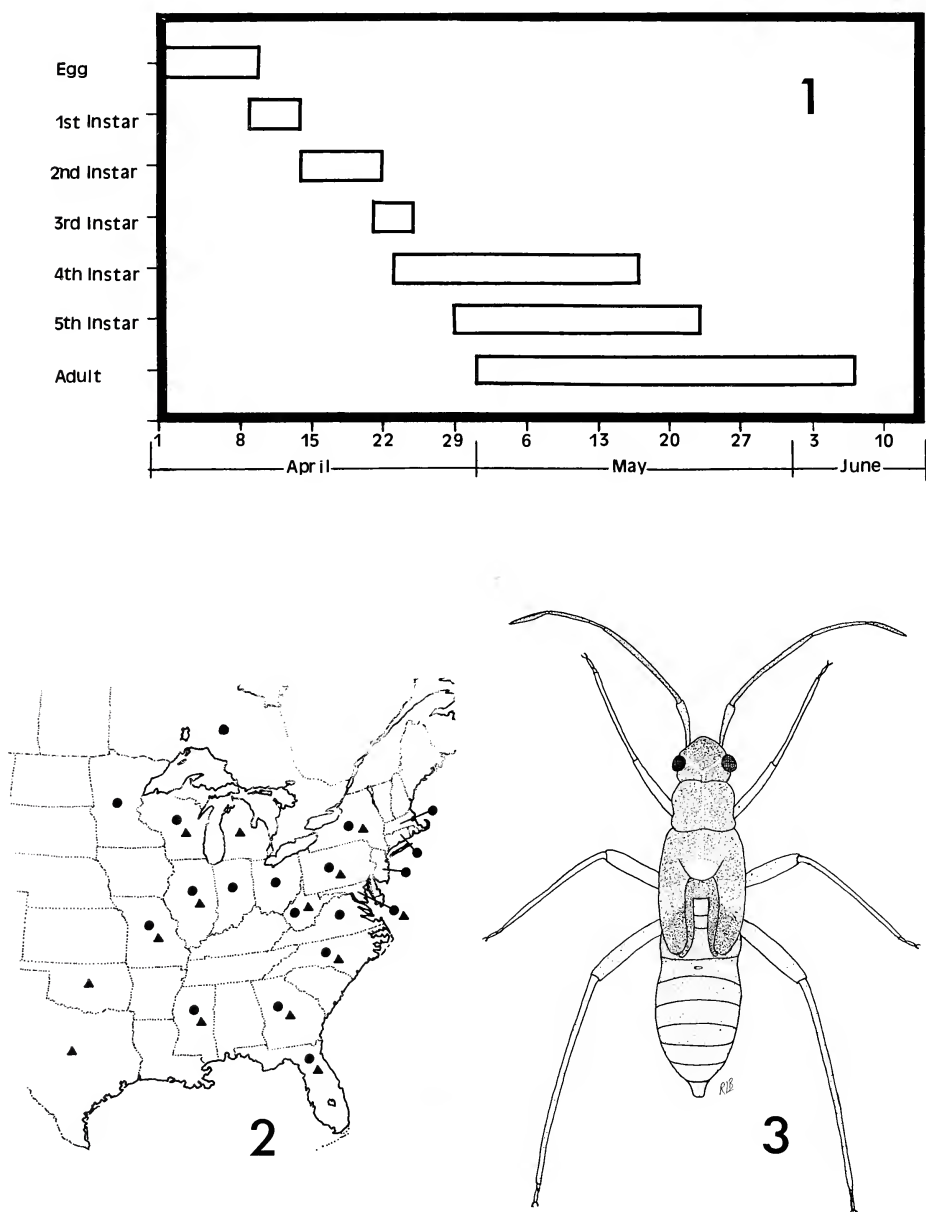
Figs. 1–3.   1. Generalized seasonal history of *Pseudoxenetus regalis* (Uhler) in central Missouri, 1984–1986. 2. North American distribution of *Pseudoxenetus regalis* (Uhler): "*regalis*" morph (closed triangles), "*scutellatus*" morph (closed circles). 3. *Pseudoxenetus regalis* (Uhler), fifth instar nymph.

1.53 mm, reaching mesocoxae; yellowish, apex of segment IV black. Antennae: with fine recumbent setae; segment I, length 0.61 mm, yellowish, red longitudinal line dorsally; II, 1.59 mm, red; III, 0.91 mm, testaceous, basal ⅓ yellowish; IV, 0.69 mm, red. Pronotum: length 0.74 mm, humeral width 0.91 mm, reddish brown, with narrow medial line pale. Scutellum white. Wingpads reddish brown reaching apex of 3rd abdominal segment. Abdomen red, variegated with pale specks, transverse band between 3rd and 4th segments and apical third of 8th segment pale, 9th and 10th segments reddish brown. Legs yellowish; pro- and mesocoxae reddish; pro- and mesofemora with brownish longitudinal line dorsally; mesotibiae brownish on ven-tro-basal half, metafemora red, apex yellowish; metatibiae red, distal third yellowish; 2nd tarsal segment reddish brown.

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MARTINIUS TEMPORALIS, A NEW SPECIES FROM ECUADOR (COLEOPTERA: LIMNICHIDAE: THAUMASTODINAE)

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Abstract.—*Martinius temporalis* is described from Ecuador. The male genitalia are figured and characters to separate it from other known species are given.

The genus *Martinius* was described by Spilman (1959) to contain a single species, *M. tellipontis,* from Panama. A second species, *M. ripisaltator* was later described from Cuba (Spilman, 1966). The species described here is the third in the genus and the first known from South America. All specimens included are part of the Ecuador-Peace Corps-Smithsonian Institution Aquatic Insect Survey. All specimens are deposited in the U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Martinius can be recognized by its shape (Fig. 1), nearly contiguous transverse eyes, seven-segmented antennae, 4-4-4 tarsal formula and long, oblique hind coxae. For a complete description of the subfamily and genus see Spilman (1959).

Martinius temporalis, new species

Description. MALE: Length 2.3–3.0 mm, width 1.2–1.4 mm, elongate oval, widest at middle, transversely shallowly convex. Black. Head densely pubescent with very short golden appressed hairs; punctation fine, obscured by pubescence, except for two short rows of close, deep, perforate punctures between the eyes. Pronotum densely pubescent with short, posteriorly directed golden hairs and evenly scattered longer erect and recurved golden hairs; giving a speckled appearance to the surface; surface rugulose where hairs are eroded. Elytral pubescence of three kinds: the short, appressed, golden hairs, the longer erect, recurved golden hairs, and patches of short, appressed to slightly erect yellow-brown hairs. The patches of yellow-brown hairs occur only on the posterior half of the elytra and produce an indistinct maculation in certain lights. Ventral pubescence very short, golden, posteriorly directed on most surfaces; surface appearing rugulose where hairs are abraded. Last visible abdominal sternum with several rows of long, coarse, brown, curved setae, encircling a roughly heart-shaped depressed area in the center of the sternum. Aedeagus with parameres parallel-sided, curving evenly inward from about half their lengths to the rounded tips; penis nearly conical, tip broadly rounded (Fig. 2).

FEMALE: Externally identical to male, except last visible sternum not depressed between rows of setae. Size averaging somewhat larger than the male.

Holotype. Male. Ecuador: Manabi, Bahia de Caraquez, brackish lagoon, 9.V.1975, Spangler, Langley, & Cohen. Allotype: Female. Same data as holotype. Paratypes: 61♂, 133♀, same data as holotype; 5♂, 7♀, Bahia [as Caraquez] 10.I.1978, Wayne N. Mathis.
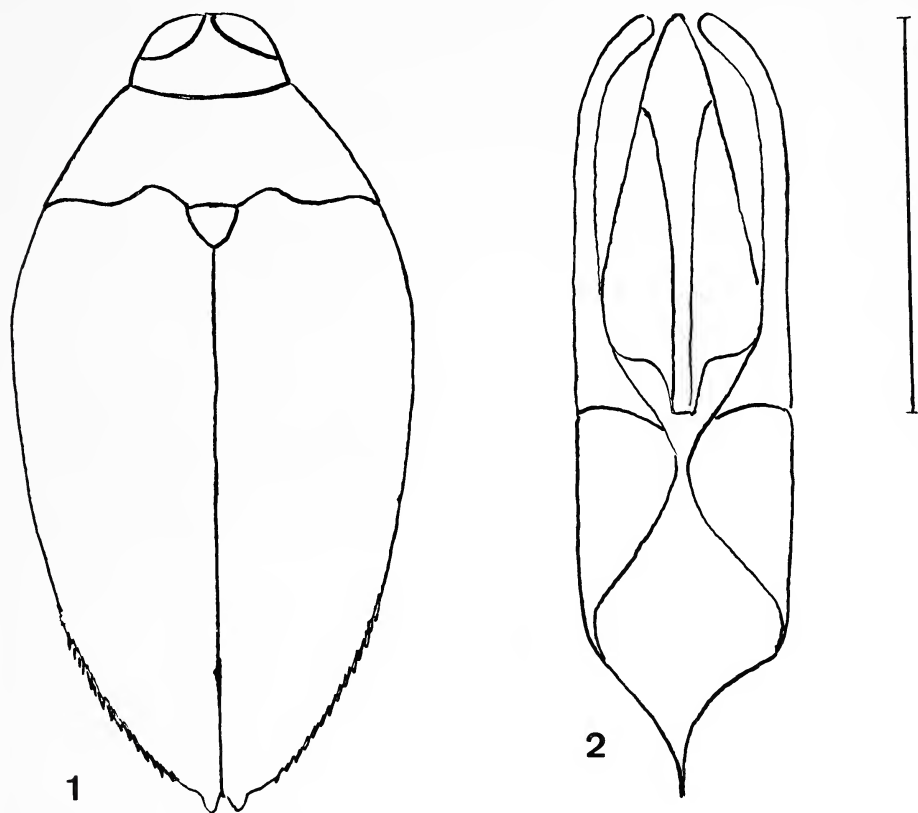
Figs. 1–2. 1. *Martinius* habitus. Approximate length 2.7 mm. 2. Male genitalia, *Martinius temporalis*. Line equals 0.25 mm.

Discussion. Martinius temporalis does not seem to be sympatric with the other known species. It can be readily distinguished from them by the lack of elytral maculations on the anterior half of the elytra and the generally indistinct character of the maculations where they do occur. In the other two species the maculations are the result of distinct differences in the color of the pubescence.

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OBSERVATIONS ON SWARMS OF
RHAMPHOMYIA SOCIABILIS (WILLISTON)
(DIPTERA: EMPIDIDAE)

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Abstract. — The swarming behavior of *Rhamphomyia sociabilis* was studied at three neighboring sites in Larimer Co., Colorado. One swarm reformed at the same site for five years, another for four years; in each case the swarm formed in mid July and persisted for about a month. Males entered the swarm carrying prey and transferred the prey to females as the latter joined the swarm. Mating pairs moved about within the swarm and were not seen to settle. Prey consisted of small insects of six orders, about 70% of the prey consisting of Diptera.

Over the past five years I have had an opportunity to observe three swarms of *Rhamphomyia sociabilis* (Williston) (Diptera: Empididae) near my home 23 km west of Livermore, Larimer Co., Colorado, at 2,370 m elevation. Although the behavior of this species does not appear to differ in any important way from that of several other known species of the genus, few persons have had an opportunity to study swarming at one site over a full season or over a period of years. Although *R. sociabilis* was described from eastern Washington and is best known from the northwestern United States (Steyskal, 1984, and pers. comm.), it is evidently locally common on the eastern slopes of the Rocky Mountains in Colorado. In addition to the swarms described here, there is a long series in the collections of Colorado State University, collected in Evergreen, Jefferson Co., Colorado, by M. T. James (determined by James as *R. abdita* Coquillett, a synonym). Evergreen is ecologically similar to the locale of the present studies and is at about the same altitude.

STUDY AREA AND METHODS

Most observations were made at a swarm site along a path leading to my house (swarm I). The swarm moved back and forth in an aisle measuring 5 by 15 m among ponderosa pines and Douglas firs. The soil beneath consisted of fine gravel, of brownish color and largely devoid of litter and vegetation. Some 40 m to the southwest there was a rocky promontory overlooking a deep valley. Since summer winds are frequently from the southwest, the area is somewhat protected from these winds. This swarm site was discovered in 1983 and observed periodically through 1986; flies were absent from it in 1987. Successive generations of flies were obviously attracted to this site.

A second swarm site (II), about 300 m away, was studied briefly each year from 1983 to 1987, a five year span. Each year, the flies came to an aisle among conifers a short distance northeast of a rocky outcrop that overlooked this same valley. However, the soil here was largely covered with pine needles and clumps of short grass. A third swarm site (III), not discovered until 1986 but also active in 1987,

was about 7 km away but again among conifers northeast of a rocky prominence. In this instance the ground was mostly covered with fairly tall grasses and wild-flowers. All three sites were essentially dry, open forest; in no case were there streams or ponds within 0.5 km. Swarm sites II and III were used for making sweep samples from various parts of the swarm to obtain sex ratios and prey specimens, while swarm site I was used for observation and subject to minimal disturbance.

Shade temperature was recorded with a mercury thermometer and wind speed with a Dwyer wind meter. Observations were made against the sky, against a dark background of trees, or against a large sheet of black cardboard placed behind the swarm. At times, parts of the swarm were dusted with talc or with white flour and the time recorded until the last marked pair disappeared from the swarm.

Voucher specimens have been placed in the collections of the U.S. National Museum and of Colorado State University.

<center>RESULTS</center>

In 1983–1986 swarms at sites I and II varied from 6 to about 50 individuals, but in 1987 the swarm at site II increased to a maximum of about 120. The swarm at site III was very large both in 1986 and 1987, numbering several hundred individuals. Larger swarms produced a distinct, low humming sound.

In 1985 swarm I was seen to form in mid June and to have disappeared by mid July. More careful observations in 1986 revealed first swarming on 16 June and last (very reduced) swarming on 19 July. Between those dates a swarm formed for at least part of every day except 26 June and 18 July, days of nearly continuous rain. During 1987, swarm II was first noted on 19 June and was last seen on 19 July. Dates of study for swarm III were 4 and 15 July 1986 and 19 June and 3 July 1987. Evidently the flight periods of all three swarms were very similar.

During heavy showers the swarms tended to disappear, although a few flies often swarmed in a light rain. Wind gusts of 8–14 km/hr often caused the swarms to be slightly displaced and disorganized, but persistent winds of over 14 km/hr resulted in disappearance of the swarms. The flies were seen to start swarming as early as 0840 hrs (Mountain Daylight Time) and to remain as late as 2000 hrs, when the sun was very low on the horizon. Shade temperature appeared to have little effect on swarming; swarms were present as low as 16°C and as high as 29°C (these are very nearly the daylight extremes experienced at this altitude during the swarming period). In general, swarms seemed to prefer at least partial shade except in the early morning or late in the day, when they tended to drift into patches of sunlight. A thin cloud cover or passing clouds had no effect on swarming. On warm, clear days there was a noticeable decline in the size of the swarms at mid-day, and occasionally no flies were present at that time; little shade was available in the aisles between 1100 and 1400 hrs.

The swarms were by no means homogenous at all times. In fact three different subswarms could be detected. Most conspicuous was subswarm *a,* consisting of mating pairs with prey; these formed a compact cluster of slow-flying pairs, 2–3 m in diameter and 1–2 m high, though occasionally drifting upward to 3 m. Within this space individual pairs moved in irregular circles, figure 8s, and up and down movements, only 10–40 cm apart but rarely contacting one another. A second sub-

swarm (*b*) consisted mostly of males carrying prey; this was a more diffuse swarm, often 3–5 m in diameter, the males flying somewhat more rapidly than was the case with mating pairs. A third subswarm (*c*) always occurred laterally to and below the others; individuals (never with prey) moved back and forth so swiftly that they seemed no more than a streak. They moved in an elongate pattern 0.5 to 1 m above the ground. This subswarm consisted mainly of females.

Sweep samples confirmed the different sex ratios in these subswarms. The best samples were obtained on 4 July 1986 in swarm III. A sweep through subswarm *a* yielded 13 males, 13 females, and 13 prey. On this date the males formed their more diffuse subswarm (*b*) about 4 m away; a sweep through this subswarm yielded 20 males, 10 females, and a few prey. Adjacent to this subswarm was an elongate area beneath tree branches, about a meter high, filled with individuals flying very swiftly back and forth. A sweep sample in this subswarm (*c*) yielded 24 females and 6 males (no prey). Only a few of these females had distended abdomens, in contrast to those in subswarm *a*, in which many females had swollen abdomens (similar to those of mosquitoes that have just had a blood meal).

Only at the largest swarm (III) did I ever observe all three subswarms at one time. At swarms I and II it was common to see a diffuse group of prey-laden males (*b*) early in the morning and often, after a mid-day hiatus, in the early afternoon. The more compact subswarms of mating pairs (*a*) formed in mid or late morning and especially in late afternoon, and at these times the swift-flying individuals could often be seen forming an elongate pattern (subswarm *c*) nearby. Evidently males capture prey early in the day, and again later in the day, and fly together in a portion of the arena (subswarm *b*). As they are joined by females, they form a more compact subswarm (*a*) in which flight is noticeably slower. The swift-flying individuals in subswarm *c* are evidently mainly females that are about to join males or have just completed mating. Thus the pattern of swarm formation appears to be:

$$♀c \rightarrow ♂b \rightarrow ♀♂a$$

Observations on several species of this genus suggest that females are not predaceous, and the only food they take is that presented to them by males. Individual females evidently enter the swarm many times in the course of their lives, possibly several times per ovarian cycle (Downes, 1969). Although in the present case swarming occurred over a 30–32 day period, I have no information on the length of life of individuals or the number of times they enter the swarm. I never observed individuals of either sex, or mating pairs, resting on the ground or on vegetation, although I made an effort to find them.

It is difficult to observe the precise details of mating, but it is clear that males transfer the prey to the females soon after they make contact. Males are above the females, which feed on the prey during the aerial mating period. The wings of both partners are in motion during the mating period. I found it impossible to follow individual pairs for more than (in one case) four minutes. However, by dusting subswarm *a* with talc or flour I was able to watch the gradual disappearance of marked pairs up to 20 minutes, after which no marked pairs were present. That copulation of individual pairs is of much shorter duration than duration of the swarm is also suggested by the fact that up to one third of prey items taken in sweeps still showed movements of body parts; evidently these had only recently been transferred

Table 1. Families of insects taken as prey by *Rhamphomyia sociabilis,* with number of specimens taken.

Ephemeroptera	Hymenoptera	Milichiidae (3)
Baetidae, male (1)	Braconidae (4)	Otitidae (1)
Psocoptera	Formicidae, males (60)	Phoridae (17)
Myopsocidae (1)	Diptera	Pipunculidae (4)
Pseudocaeciliidae (1)	Agromyzidae (4)	Psilidae (3)
Hemiptera	Anthomyidae (35)	Scatopsidae (2)
Aphididae, alate (1)	Bombyliidae (4)	Scenopinidae (6)
Cicadellidae (18)	Cecidomyidae (1)	Sciaridae (16)
Delphacidae (1)	Chironomidae (13)	Sepsidae (6)
Miridae (15)	Chloropidae (23)	Simuliidae (17)
Psyillidae (5)	Dolichopodidae (13)	Sphaeroceridae (3)
Lepidoptera	Drosophilidae (2)	Stratiomyidae (6)
Psychidae (1)	Empididae (18)	Tachinidae (15)
	Ephydridae (4)	Tephritidae (1)
	Lauxaniidae (9)	Tipulidae (1)

to females. Other prey items in sweep samples were dead and in some cases shriveled and distorted. It is possible that some of these had been used a second time, as reported for a species of *Empis* by Hamm (1909).

Prey items varied considerably in size. Sixty-eight prey items, taken in swarm III on 4 July, varied in length from 2.0 to 4.5 mm (mean 3.3 mm). The longest prey I took from a swarm at any time was a male chironomid midge measuring 5 mm and thus about the same length as the empidid that carried it, though more slender. The bulkiest prey was a small moth with a body length of 3.5 mm and a wing length of 4.3 mm. Male ants were the most frequently taken type of prey, but they occurred only in swarm III, which was evidently near ant colonies. Diptera made up about 70% of the combined prey of the three swarms. It is interesting that although Empididae were used as prey fairly often, none of them were *Rhamphomyia sociabilis.* The list of prey (Table 1) is very similar to lists published for *R. scutellaris* Coquillett (Crane, 1961), for *R. curvipes* Coquillett (Powell, 1964), and for *R. longicauda* Loew (Steyskal, 1942, 1950; Newkirk, 1970). The 335 prey records represent 37 families of six orders. This compares with 20 families of four orders reported for *curvipes* and 29 families of six orders reported for *scutellaris. R. longicauda* is reported to use insects of six orders, with one record of a spider (Newkirk, 1970). In each case Diptera made up the majority of the prey.

DISCUSSION

The swarming behavior of *R. sociabilis* resembles closely that of *R. curvipes* as described by Powell (1964). The latter species, observed over a lawn adjacent to a hedge in Contra Costa Co., California, also showed a group of slow-flying, prey-bearing pairs and an adjacent subswarm of individuals (mainly females) flying very rapidly in elongate patterns; however, these flew higher than the mating pairs rather

than lower as in *sociabilis.* Most swarming was in the morning and late afternoon. Powell found the swarms at the same site in two successive years.

The observations of Crane (1961) on *R. scutellaris* extended over three years, the flies occurring each year over two sections of a trail near San Jose, California. He found that males bearing prey often alighted on bushes in the swarm area and that mated pairs left the swarm area, flying out of sight while still coupled. One pair remained in the swarm for 25 minutes before leaving. Alcock et al. (1979) found *R. pectoris* Coquillett swarming over pools of water and depressions in sandy roads on St. Catherine's Island, Georgia. Swarms formed in the evening on each of three days; at first they consisted of males, mostly with prey, but females soon joined and contacted the males. Copulation was apparently completed in flight. These authors surmised that non-prey-carrying males might intervene during prey transfer and usurp a female and prey from a competitor. I did not observe males without prey in swarms of *R. sociabilis.*

The behavior of *R. longicauda,* a species widespread in eastern North America, differs in certain particulars (Steyskal, 1941, 1942, 1950; Newkirk, 1970; also J. A. Downes and D. H. Funk, pers. comm.). In this species, swarms of females form at dusk in open places adjacent to vegetation or buildings. The females inflate their abdomens with air such that the pleural membranes are greatly stretched; the abdomen collapses upon being punctured. The legs, which are provided with series of scale-like setae as in many members of the genus, embrace the abdomen laterally (Steyskal, 1941, provides a sketch). The expanded abdomen and legs together apparently produce a large signal to which the males respond. This expansion of the abdomen is far greater than I have observed in *sociabilis* and probably not analogous to the distention I have interpreted as the result of engorgement. No unusual distention of the abdomen has been reported in *curvipes, scutellaris,* or *pectoris.*

It is clear that there is much variation within the genus. Downes (1970) presented a description of the swarming of *R. nigrita* Zetterstedt on Ellesmere Island, in northern Canada. This species swarms over markers such as piles of debris; mating is completed after the pair settles on a nearby object. Mating lasted 38 and 48 minutes in two observed cases. Another arctic species, *R. ursinella* Melander, is virtually non-flying and mating occurs on the ground. Downes (1970) discussed interspecific variation in several other species of the genus.

Chvála, in his review of swarming and mating in Empididae (1976) states that the sexes meet in the swarm but that mating pairs leave the swarm to complete copulation. I observed no mating pairs of *R. sociabilis* outside the swarm and gained the impression that females were leaving the swarm only after copulation was completed.

Although some species (such as *pectoris* and *nigrita*) respond to swarm markers on the ground, the situation in *sociabilis, scutellaris, curvipes,* and *longicauda* appears somewhat different. Each of these species reappeared each year at an arena consisting of a more or less uniform substrate flanked by vegetation and with an opening to the sky above. Crane (1961) states that he studied other parts of the trail where *scutellaris* was found, but discovered no other swarms. I explored other sites among conifers northeast of rocky promontories, seemingly very similar to sites occupied by *sociabilis* swarms, but without result. Yet there were differences in the three swarm sites, differences in ground cover and in the arrangement of trees (swarm II was in a shadier site than I, while III was in a more open site, with more widely spaced

trees). Yet these sites had certain features to which the flies responded (presumably visually) year after year.

As with most Empididae, the eyes of the male *R. sociabilis* are contiguous and are divided into an upper part with large facets and a lower part with small facets. In several species of Empididae it has been reported that the male approaches the female from below, then holds a position a few cm away and flies in unison with her before coupling (Downes, 1970). The enlarged facets of the upper part of the eyes are believed to play a role in this close maneuvering by the male. The lower facets (which are like those of the female) are evidently concerned with behavior common to both sexes (Downes, 1969; Chvála, 1976).

The legs of the females of *R. sociabilis* and several other species are fringed with large, scale-like setae, not present in males. Downes (1970) suggests that females may display to males before pairing. In *sociabilis* the legs of the female appear to hang downward, where they occasionally glitter in the light. In *longicauda* the legs are held laterally and enhance the breadth of the inflated abdomen. Frohne (1959) mentions an unidentified Alaskan species of *Rhamphomyia* in which the female is "garishly marked with an extensive silvery abdominal 'saddle' which flashes conspicuously as she crosses beams of sunlight." It seems very probable that females of several species of this genus do indeed display, behavior possibly permitting them to select from among the responding males one with a particularly attractive prey item.

It is interesting that males of *R. sociabilis* used Empididae as prey fairly frequently (Table 1) but were not found to use conspecifics. Cannibalism has, however, been reported in *R. scutellaris* (Crane, 1961) and in *Empis trigramma* (Hamm, 1933). In some species of *Rhamphomyia*, males do much of their hunting at swarms of other Diptera, such as mosquitoes (Downes, 1970, and his fig. 1). Considering the great diversity of prey taken by males of *sociabilis*, it seems likely that the males hunt over a wide area.

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DROSOPHILA (*HIRTODROSOPHILA*) *CHANDLERI* (DIPTERA: DROSOPHILIDAE) A NEW SPECIES FROM SRI LANKA WITH BROAD-HEADED MALES

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Abstract.—A new species from Sri Lanka, closely related to *Drosophila* (*H.*) *caputudis* (Grimaldi, 1986), is described and named *Drosophila chandleri*. Males have two very distinctive morphological features: a broad head, which is a result of expanded frontal-orbital plates and face, and a patch of very large, scaliform, interfacetal setulae in the middle of each eye.

The purpose of this paper is to describe a new species of drosophilid so as to make the name available for a paper being prepared on the repeated evolution of broad-headed males in the Drosophilidae and other Diptera.

Drosophila (Hirtodrosophila) chandleri, new species
Figs. 1–2b

Diagnosis. Very similar to *Drosophila caputudis* with the exception of the following: in both sexes abdomen completely dark black-brown, halter knob light brown and blended into pleural stripe; all of notum, postscutellum, postnotum, and most of scutellum dark brown; front of head mostly dark brown, face dark brown with light cream-colored, modest carina. In males oral margin with light stripe; clypeus, katepisternum, and all legs light cream-colored. In the females oral margin, clypeus, and portions of katepisternum and legs brown. Males with patch of long, stout, scaliform interfacetal setulae on eye, head about 1⅓ times the width of female head. Male and female terminalia as figured and discussed in description.

Description. Male head width 1⅓–1½ times the thorax width; head of female only slightly wider than thorax. Head in both sexes almost entirely dark brown; carina barely present, light yellow. Oral margin light in male, dark in female, rest of face (except carina) dark brown. Eyes dark red, with dense interfacetal setulae. Male with apical patch of interfacetal setulae modified into scales. Clypeus dark brown in female, light yellow in male. In both sexes palpi, proboscis, and cheeks light yellow; gena, postocciput, and antenna dark brown. Arista with 6–7 dorsal and 2 ventral branches. Ratio of lengths of orbital setae: anterior reclinate (1); proclinate (2): posterior reclinate (6). Proclinate medial to anterior reclinate by distance one-half length of anterior reclinate. Postocellars cruciate.

Male legs unicolorous light yellow; pleura mostly light yellow, with brown band at notopleural suture, running length of thorax. Female with middle three-fifths of femur diffuse brown, remaining portion of legs light yellow; most of pleuron dark brown. In both sexes, halter, notum, scutellum, subscutellum, and postnotum dark brown; all abdominal tergites black, sternites yellow. Wing hyaline, without markings. Spermathecal capsule subspherical and smooth, introvert annulate, slight swelling
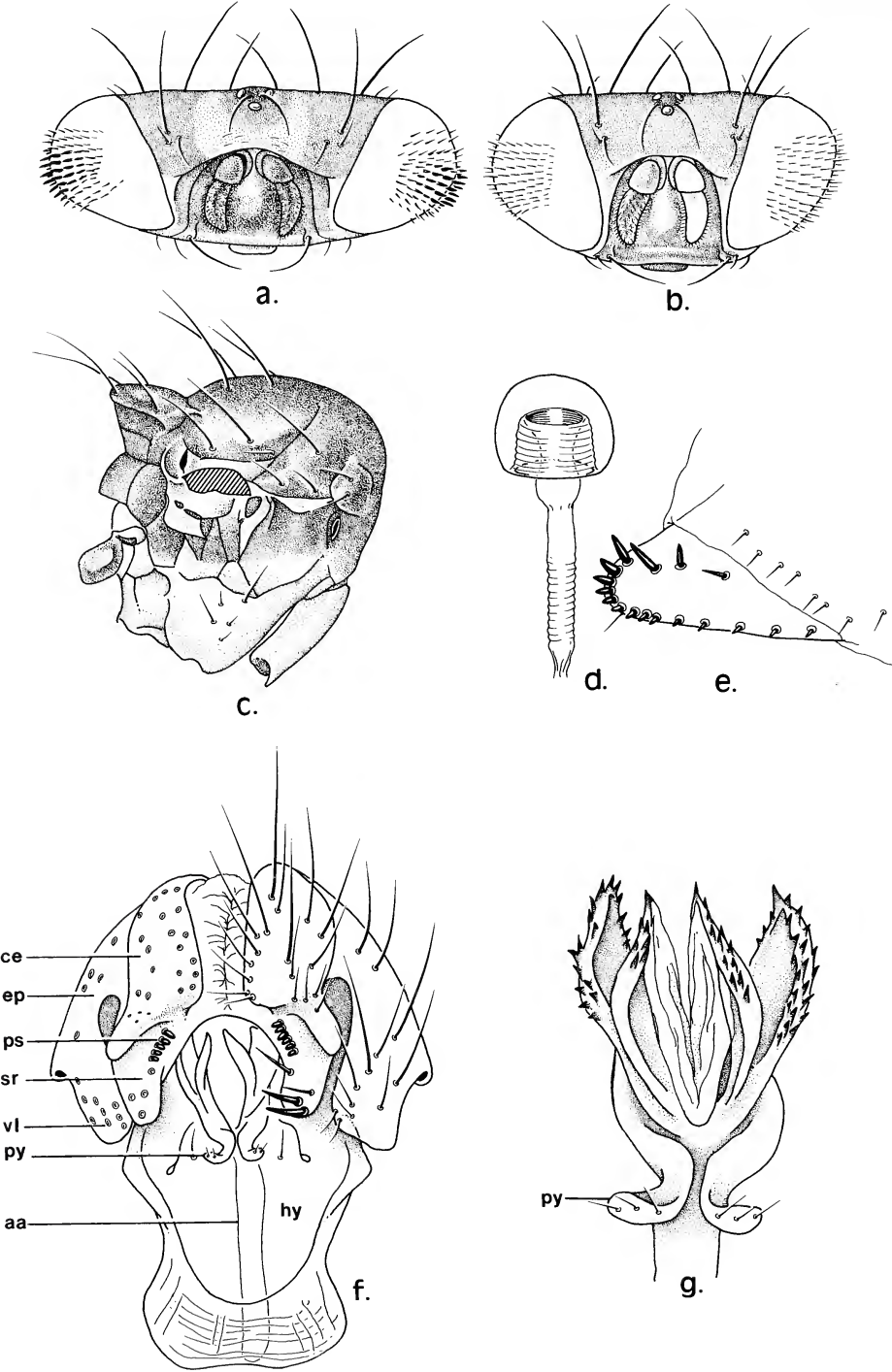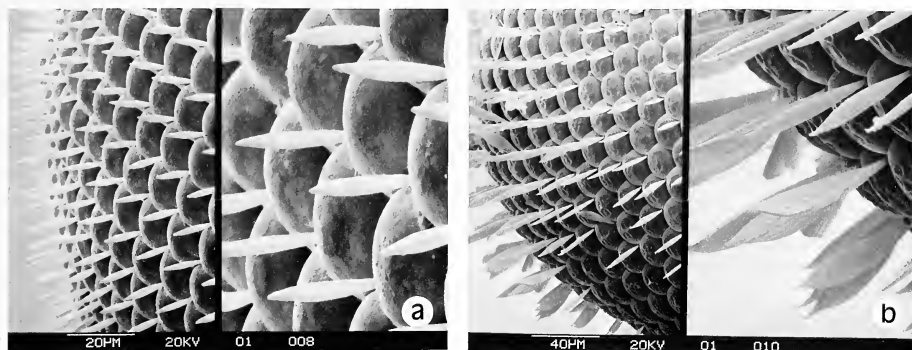
Fig. 2. Scanning electron micrographs of male *Drosophila* (*Hirtodrosophila*) species eye setulae: a. *Drosophila* (*H.*) sp. from Guyana, near *D.* (*H.*) *thoracis*. b. *D.* (*H.*) *chandleri*. Magnified view for each specimen taken of setulae at apex of eye. Note that magnification for *D. chandleri* is one-half that of specimen in Fig. 2a.

present on neck of spermathecal duct near opening to introvert. Oviscape short and broad in lateral view, with 17 ovisensilla pegs: 8 short ones on ventral margin anterior to sensilla hair, 5 equally short and longer ones posterior to sensilla hair, and 4 long ones near dorsal surface.

Epandrium and cercus, dark brown, each with well-developed ventral lobe. Surstylus about as large as ventral epandrial lobe, with 2 types of prensisetae separated into 2 fields: a dorsal row of 5–6 short, stout ones and 4 long, thin ones ventrally. Lateral margins of hypandrium deeply indented, anterior margin less so. Paraphysis small, with 3 minute setulae. Aedeagal apodeme extended to anterior margin of hypandrium. Distiphallus with 4 lobes and each bearing minute scales on apical half.

Measurements. Holotype male: Head Width (HW) = 1.09 mm, Thorax Length (THL) = 0.88. Paratype male: HW = 1.33, THL = 0.88. Paratype female: HW = 1.04, THL = 0.98.

Holotype. Male: Sri Lanka: Labugama, 18/II/74, P. J. Chandler "Forest," (not dissected) in the American Museum of Natural History.

Paratypes. One male, one female (terminalia of each dissected), collected at same time and locality as holotype (also in AMNH).

Etymology. Patronym, named for the collector, Mr. Peter J. Chandler of Weston Research Laboratories, Maidenhead, Berks, England.

Discussion. The features of *D. chandleri* that show it has a close relationship with *D. caputudis* are the following: the manner in which the male head is broadened, and the extent of the modification; proclinate orbital seta considerably medial to the

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Fig. 1. *Drosophila* (*H.*) *chandleri*: a. Male head. b. Female head. c. Lateral view of male thorax (wing is removed). d. Spermatheca. e. Lateral view of oviscape. f. Ventral view of male terminalia. aa, aedeagal apodeme; ce, cercus; ep, epandrium; hy, hypandrium; ps, prensisetae; py, paraphysis; vl, ventral lobe (of epandrium). g. Detail of distiphallus, showing lobes and scalation.

anterior reclinate and at about the same level; posterior reclinates very long; notum dark, both species with at least a portion of the pleura near the wing darkened; oviscape with ovisensilla pegs at dorsal margin much longer than the ones on the ventral margin; in the male, the ventral epandrial lobe is well-developed, 2 types of prensisetae exist (a row of short, stout ones, and some long, narrow ones at the surstylar apex), distiphallus has 4 lobes and bears minute scales. Scaliform eye setulae are autapomorphic for the Drosophilidae. To my knowledge, this trait occurs only in *Diopsosoma* (Periscelididae), another (albeit unrelated) broad-headed fly.

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REPRODUCTIVE DIFFERENCES BETWEEN *RHAGOLETIS* (DIPTERA: TEPHRITIDAE) FRUIT PARASITES OF *CORNUS AMOMUM* AND *C. FLORIDA* (CORNACEAE)

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Abstract.—Two *Rhagoletis* fruit parasites of dogwood, previously thought to be conspecific, are shown to be reproductively distinct. Laboratory studies show consistent differences in the flies' oviposition response to the respective host fruits and in production of viable F$_1$ hybrid first instar larvae. The specific status of the fly populations is discussed.

The four members of the *Rhagoletis pomonella* (Walsh) species group of true fruit flies (Diptera: Tephritidae) have been at the forefront of discussions concerning modes of host race formation and speciation. A sympatric model (Bush, 1969a) is based upon the assumption that mating and oviposition by each of these morphologically similar univoltine species of fruit parasites occur on plants in a different family. This model assumes that adult selection and larval use (larvae are confined to feeding on the fruit in which eggs were deposited) of a host plant are strongly affected by factors that are more similar within than among plant families and, therefore, that the recent colonization of a plant species in a novel family affords a considerable measure of reproductive isolation from the parental fly population. While the members of the *Rhagoletis suavis* (Loew) species group, for example, probably diverged in allopatry (now overlapping discontinuously in geographic range but entirely in host range [*Juglans* spp.: Juglandaceae]) and maintained reproductive integrity through variation in morphological characters involved with mate selection, divergence in host plant family association apparently provided the initial reproductive isolation that allowed for subsequent speciation of new host-associated populations from the ancestral form in the *R. pomonella* group (Bush, 1969b).

A reasonable prediction from the model above is that similar looking fruit flies attacking members of the same plant family are more likely to be conspecific than are those attacking heterofamilial plants. However, this appears to be contradicted by the existence of several populations of *Rhagoletis* flies on different dogwoods (*Cornus*: Cornaceae). *Rhagoletis electromorpha* Berlocher was recently described from flies that were reared from *C. drummondii* C. A. Meyer and *C. rasemosa* Lam. and were once considered conspecific with *R. tabellaria* (Fitch) flies collected from *C. stolonifera* Michx. (Berlocher, 1984) and *C. amomum* Mill. (Bush, 1966). A second example of host family overlap is provided by this study.

A population of *Rhagoletis* flies feeding on flowering dogwood (*Cornus florida* L.) was first noted by Benjamin (1934). The flowering dogwood fly is visually identical with *R. cornivora* Bush (the member of the *R. pomonella* sibling species group which infests *C. amomum, C. canadensis* L. [Bush, 1966] and *C. racemosa* [Smith, unpubl.]) and the two occur in partial sympatry in eastern North America (Bush, 1966). The logic of the sympatric speciation argument, as envisioned for this group of fruit flies,

dictates that these two *Cornus*-infesting flies are conspecific. However, electrophoretic enzyme analyses indicate that the flowering dogwood fly is much more closely related to *R. pomonella* than is *R. cornivora* (Berlocher, 1976; Smith, 1986). Although Berlocher (1976) suggested that these two dogwood flies were distinct, the data did not eliminate the possibility that differences in fruit chemistry may select for particular larval genotypes. This study demonstrates that *R. cornivora* and the flowering dogwood fly indeed are heterospecific, based on differences in reproductive biology related to host selection and to egg hatch success of test crosses.

MATERIALS AND METHODS

The *Rhagoletis* fruit parasites used in this study were collected from natural populations in eastern Illinois. *Rhagoletis cornivora* flies were from silky dogwood, *C. amomum,* in Champaign and flowering dogwood flies were from Fairfield. The *R. pomonella* flies used in the test of egg hatch success were collected in Urbana from downy hawthorn (*Crataegus mollis* [T. & G.] Scheele: Rosaceae). Infested fruits were placed in the laboratory on hardware cloth over moist vermiculite, in which exiting larvae pupated prior to spending diapause in cold storage at 5°C until needed. After removal from the cold, pupae were placed in an environmental chamber at 24°C, 50 ± 5% relative humidity and 20:4 (L:D) photoperiod. Flies were caged separately by population (and also by sex for those to be used in test crosses) and were provided with a constant source of water and food (enzymatic yeast hydrolysate and brown sugar). Flies were first tested when ca. 4 weeks old and presumably were sexually mature. Maturity was indicated by the continued presence of copulating pairs in mixed-sex cages, by male-male copulatory attempts in unisexual cages and by female (virgin and mated) oviposition into artificial fruit consisting of hollow black hemispheres of ceresin wax (Prokopy and Bush, 1973). Eggs were attached to the inner surface of the wax domes during oviposition, facilitating their detection and removal. Females from mixed-sex cages were assumed to be mated by the time that they were tested on fruit.

In the first procedure, 50 naive (no previous exposure to real fruit) mated females were selected randomly from each dogwood population and individually tested for oviposition response to single uninfested fruit clusters of freshly-picked *Cornum amomum* (5–10 fruit per cluster, each fruit ca. 5–10 mm diameter) and *C. florida* (3–6 fruit per cluster, each fruit ca. 8–12 mm diameter), whose stems were placed in a small vial of water to prevent dessication. Females were deprived of the wax dome oviposition substrates for 18 hours prior to fruit testing. Half of the test flies from each population were offered *C. amomum* first and *C. florida* second; the other half were offered fruits in the reverse order. Females were observed on the fruit until they oviposited into or left the fruit or until 15 minutes had elapsed without oviposition, in which case they were recorded as rejecting the fruit. Females were tested on the next fruit between 20–30 minutes after their previous exposure. All females were tested in only one trial sequence. The test result of each female was placed in one of the following categories of response to these two hosts: (a) accept only its own natural fruit; (b) accept only the other fly's natural fruit; (c) accept both fruits; (d) accept neither fruit. A female that oviposited into the first fruit but rejected the second was then offered the first fruit type again. If she rejected it this time, then she was recorded

as accepting neither fruit (response "d"). This was to ensure against a false negative response to the second fruit by a female that may have deposited her last mature egg into the first fruit and simply had no more available at that time for succeeding tests.

Rhagoletis eggs are deposited in punctures produced in the fruit by the extensible sclerotized ovipositor. Females sometimes either fail to deposit an egg in a puncture or fail to produce a puncture on a given attempt. Oviposition was suggested during observations when a female withdrew the ovipositor from the fruit puncture and dragged it over the fruit surface, depositing an oviposition-deterring pheromone (Prokopy et al., 1976). However, oviposition was recorded only after fruit dissection revealed an egg. All punctures were dissected for eggs, even those made by non-dragging females.

In the second procedure, mated flies from each dogwood population were placed in clear plastic cylindrical fiberglas-screened cages (8 cm diameter, 10 cm tall) containing food, water and one mature freshly-picked Golden Delicious variety apple, *Malus pumila* Mill. (Rosaceae) (each fruit ca. 59–67 mm diameter). Each of the 20 cages per fly population contained one female and one male. At the end the first day, the apples were replaced and any ovipositor punctures were dissected for the presence of eggs. After two weeks of constant exposure to apples, another one-day count of eggs was obtained for each cage.

In the final procedure, 10 single-pair crosses of virgin flies from the two dogwood populations and from a hawthorn population of *R. pomonella* were performed for each of seven mating combinations (Table 1) in individual cages supplied with food, water and wax domes of 12 mm and 18 mm diameters. These domes were placed over moist cotton to reduce the chance of dessication of eggs deposited into them. Only pairs observed in copulation for at least 15 minutes were used for egg hatch analysis. This copulation period is usually sufficient for successful sperm transfer in *R. pomonella* (Smith and McPheron, unpubl.). Males were left in the cages to permit additional mating during the period of egg collection, which lasted for 3 weeks for some cages. All pairs were casually observed in copulation at least twice more during this period. Eggs from each cage were removed daily from the inner surface of the domes with a fine brush and transferred to individual petri dishes containing moist filter paper. Hatching usually occurred within 2–6 days. If a larva did not develop within two weeks of egg collection, then the egg was recorded as unhatched. Data were subjected to analysis of variance and differences among means were determined by a Student-Newman-Keuls' test.

RESULTS AND DISCUSSION

In the measure of oviposition response to the two dogwood fruits, each fly population demonstrated fidelity to its natural host. Of the 50 females tested from each population, (a) 35 *R. cornivora* and 33 flowering dogwood flies oviposited only into their respective hosts, while (b) none accepted only the other fly's host. Only (c) two *R. cornivora* and six flowering dogwood flies accepted both fruits, while (d) 13 and 11, respectively, accepted neither fruit (see Methods for description of response category "d"). This host fruit fidelity generally agrees with similar tests (Smith, 1986) comparing flowering dogwood flies with *R. pomonella* flies from downy hawthorn.

Table 1.   Mean proportions of hatched eggs from laboratory crosses of *R. cornivora* (cor), flowering dogwood flies (flo) and *R. pomonella* flies from hawthorn (haw). N = 10 for each mating combination. Means that are followed by the same letter are not significantly different by a Student-Newman-Keuls' test at P = 0.05.

Female × male	Eggs	Mean ± SEM
cor × cor	220	0.851 ± 0.043 a
cor × flo	213	0.023 ± 0.015 b
flo × cor	283	0.042 ± 0.014 b
flo × flo	318	0.940 ± 0.026 a
flo × haw	237	0.923 ± 0.029 a
haw × flo	287	0.919 ± 0.035 a
haw × haw	292	0.935 ± 0.031 a

However, a greater proportion of flowering dogwood fly eggs were deposited in the heterofamilial hawthorn fruit (ca. 43%) in that study than in the confamilial silky dogwood fruit (ca. 10%) here. A speculative explanation for this apparent anomaly follows from the observation that flowering dogwood flies oviposited into hawthorn fruit significantly more often than hawthorn flies did into flowering dogwood fruit (Smith, 1986). Perhaps the flowering dogwood fly descended from a hawthorn fly population and retained some degree of positive response to an ancestral host. Perhaps for the same reason, the apple-infesting population of *R. pomonella* responds even more strongly in the laboratory to its presumed ancestral hawthorn host (Walsh, 1867; Bush, 1966) than it does to apple itself (Prokopy et al., 1982; Smith, unpubl.).

In the oviposition assay with apples, none of the 20 cages of flies from either population had eggs after the first day. However, after two weeks of exposure to apple, 16 of 20 flowering dogwood fly cages yielded eggs (73 total) in the one day trial, but none of the *R. cornivora* cages did so. Thus, the flowering dogwood flies displayed a greater tendency to oviposit in apple than did *R. cornivora* flies (Mann-Whitney $U = 360$, two-tailed $P < .002$). Additional tests have shown that, even after long-term exposure to apples that have been artificially punctured with an insect pin, *R. cornivora* flies failed to oviposit in freshly-picked or in cold-stored apples and also spent little time on this relatively large fruit (Smith, 1986, and unpubl.). The results of fruit tests suggest that flowering dogwood flies may have (1) a lower threshold of induction for oviposition in novel fruit, in general, than do *R. cornivora* flies and/ or (2) a lower threshold response to rosaceous fruit (e.g., apple and hawthorn), in particular.

The egg hatch results (Table 1) indicate that these two dogwood fly populations are not reproductively compatible. Interpopulational crosses produced far lower proportions of hatching eggs than did intrapopulational ones. The lower hatch success of *R. cornivora* eggs, which appear smaller than eggs of the other members of the species group, may result from a higher level of desiccation (or other damage) resulting from deposition into the wax domes. Thus, the overall proportion of *R. cornivora* × *R. cornivora* eggs that hatched may have been higher here (82% vs. 51%) than in Smith (1986) because of greater care here to reduce desiccation. As discussed in Smith

(1986), the specific mechanism(s) responsible for the reduction in heterospecific egg hatch is unknown.

The results of this study confirm the conclusion of Berlocher (1976) that the population of *Rhagoletis* flies on flowering dogwood is not conspecific with *R. cornivora*. Evidence from enzyme electrophoresis and from analyses of reproductive biology (mating propensity and egg hatch) suggest that this population is closely related to *R. pomonella* but still may be at least partly isolated from it by differences in host selection and seasonal availability (Smith, 1986). However, because the flowering dogwood flies tested were from an edge of the host's geographic range, these differences with *R. pomonella* from hawthorn may not be consistent with those from a more central (southern) part of the flowering dogwood range. Therefore, the flowering dogwood fly should be considered to be a host-associated population of *R. pomonella* at least until further population data become available.

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NEW SPECIES AND RECORDS OF
COSTA RICAN *POLYCENTROPUS*
(TRICHOPTERA: POLYCENTROPODIDAE)

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Abstract. — Five new species of *Polycentropus* (Trichoptera: Polycentropodidae) from Costa Rica are described and illustrated: *P. fasthi, P. fortispinus, P. nebulosus, P. volcanus,* and *P. zurqui.* In addition, *P. digitus* Yamamoto, *P. fortunus* Flint, and *P. mayanus* Flint are recorded from Costa Rica for the first time. Also, *P. acanthogaster* Flint, *P. altmani* Yamamoto, *P. costaricensis* Flint, *P. dentoides* Yamamoto, *P. lingulatus* Flint, and *P. spicatus* Yamamoto occur or are likely to occur in the country.

In Costa Rica, caddisflies of the genus *Polycentropus* are restricted in distribution to small–medium sized streams in wet, forested areas, generally above 600 meters elevation. These streams are for the most part clear, cool, and fast flowing and are relatively free from pollution (Figs. 1, 2). Hamilton (1986) presented a review of the systematics and biogeography of New World *Polycentropus,* including the descriptions of 11 new Neotropical species. Collections made in Costa Rica in 1986 and 1987 revealed five additional new species not covered by Hamilton (1986) as well as several new distribution records of previously described species. These specimens support our contention that the Neotropics harbor an unexpectedly rich *Polycentropus* fauna. In this paper, we provide descriptions of these five new species along with distribution records and notes for other *Polycentropus* known (7 species) or likely (2 species) to occur in Costa Rica. Additional collecting, especially in the more remote, mountainous areas of Costa Rica will undoubtedly yield additional new species.

Morphological terminology follows Hamilton (1986). Types are deposited in the collections of the Museo Nacional de Costa Rica, San José (MNCR); the U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH); and the University of Minnesota Insect Collection, St. Paul (UMSP); as indicated below. All specimens of previously described species upon which new records are based are deposited in UMSP.

Polycentropus fasthi, new species
Fig. 3

Diagnosis. This species is closest to *P. mayanus* Flint differing most noticeably from that species in the shape of the preanal appendages. In the new species, the mesoventral processes of the preanal appendages are elongate and form sharp points (in this feature *P. fasthi* resembles *P. gertschi* Denning and *P. alatus* Flint). The inferior appendages of *P. fasthi* and *P. mayanus* are similar except that the apicomesal processes of these appendages are much less pronounced in the former species.
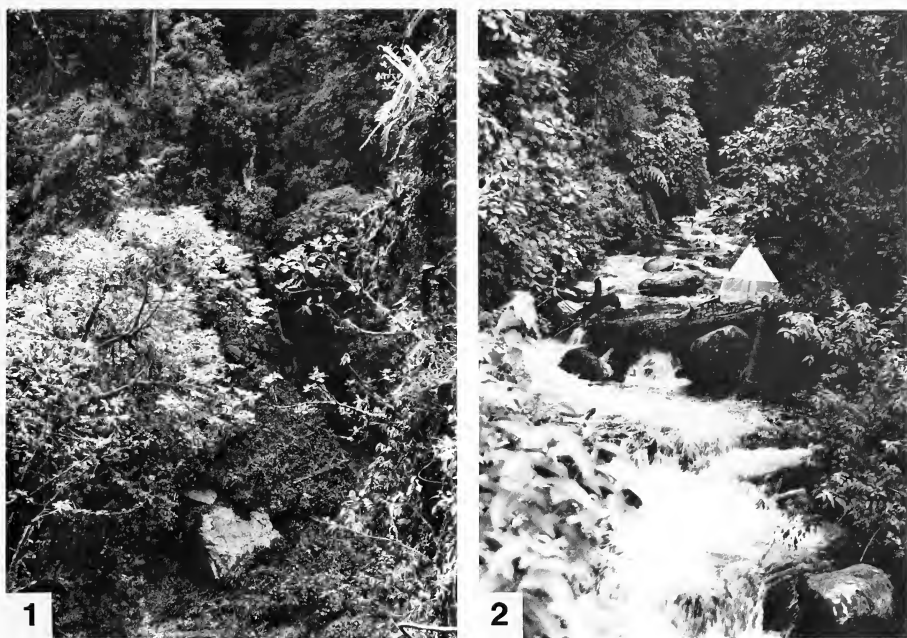
Figs. 1, 2. Habitats: 1. headwaters of Río Zurquí at 1,650 meters elevation, lower montane rainforest, Parque Nacional Braulio Carrillo, San José Province. 2. Río Bellavista at 1,400 meters elevation, premontane wet forest, Cordillera de Talamanca, Puntarenas Province.

Additionally, the apicoventral process of the phallus is longer and thinner and the phallic sclerite is shorter in *P. fasthi* than in *P. mayanus*. It is a member of the *bartolus* complex of the *gertschi* group.

Description. Male: Forewing length 5.5–6.5 mm. Body sclerites and setae generally pale brown dorsally, yellow ventrally; legs, especially femora and tarsi, with fine, dark brown setae; dorsum of head and thorax dark brown with long, erect, brown setae; forewings covered with fine, dark brown setae and with numerous small, scattered patches of golden setae; forewing bases with long, erect, dark setae. Genitalia as in Figure 3. Abdominal sternite IX large, about ⅔ height of abdominal segment VIII; in lateral view approximately circular, in ventral view approximately rectangular, slightly wider than long. Intermediate appendages of moderate length and thickness, curved mesally, apices pointed, apicomesal regions membranous. Preanal appendages approximately circular, small; mesoventral processes broad, apices attenuated, directed caudomesally. Inferior appendages relatively short; in lateral view, oval shaped, with no sharp angles or points; in ventral view, generally oval with small, apicomesal points, mesal surfaces only slightly convex. Phallus with short phallobase, apicodorsal portion mostly membranous; phallobase with narrow apicoventral process directed posteriorly then posteroventrally; single, large phallic spine present; in dorsal view, phallic sclerite broad basally, slightly expanded posteriorly and forked apically; subphallic sclerite small, forming shallow "U."

Type material. Holotype: Male, Costa Rica: Guanacaste: Parque Nacional Rincón
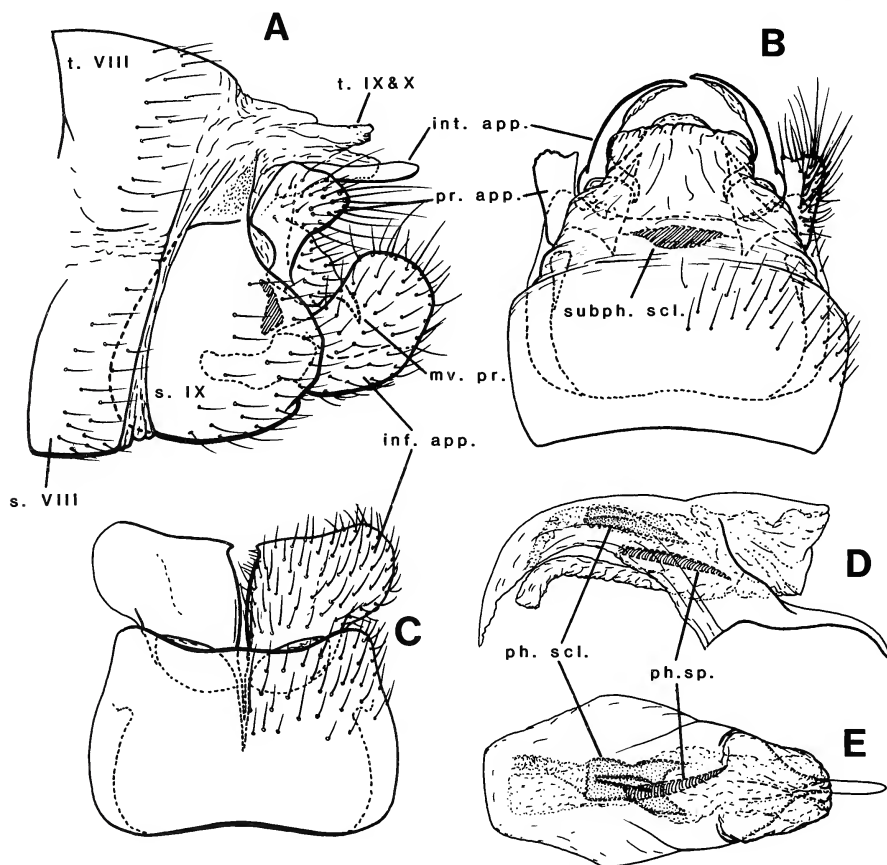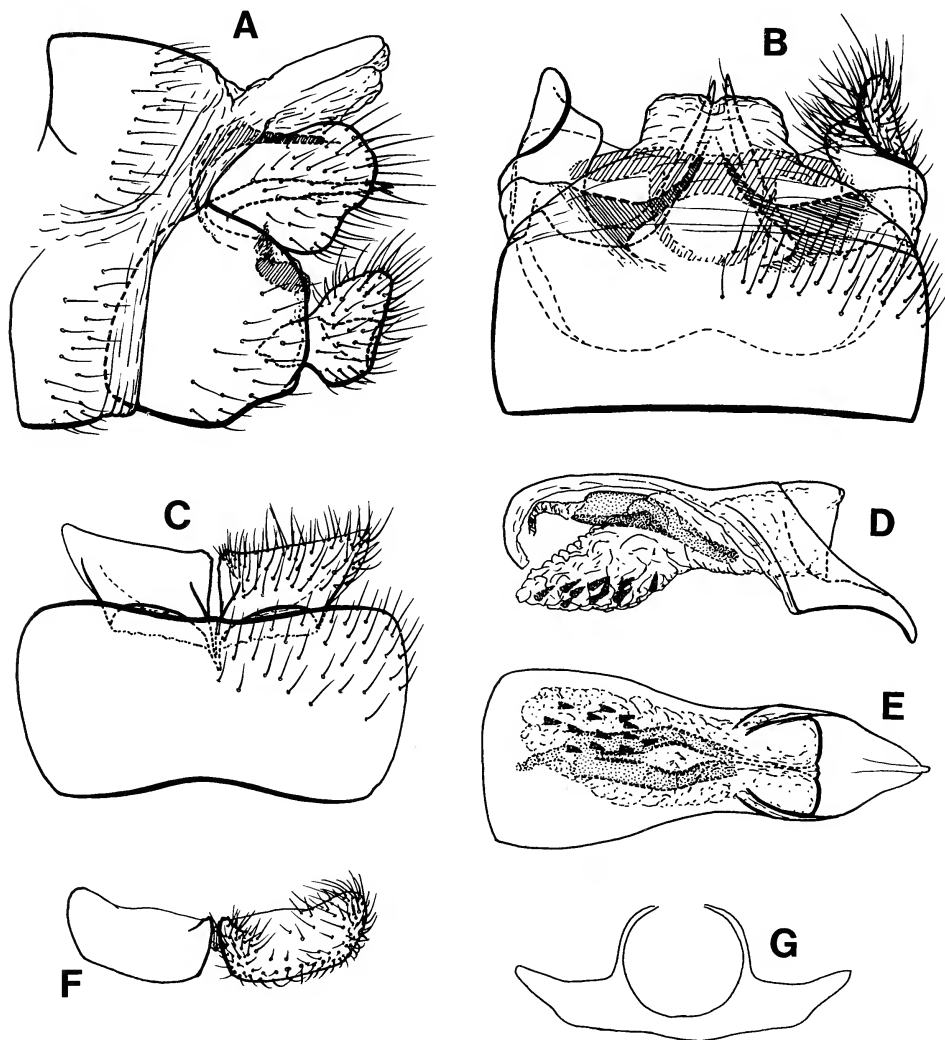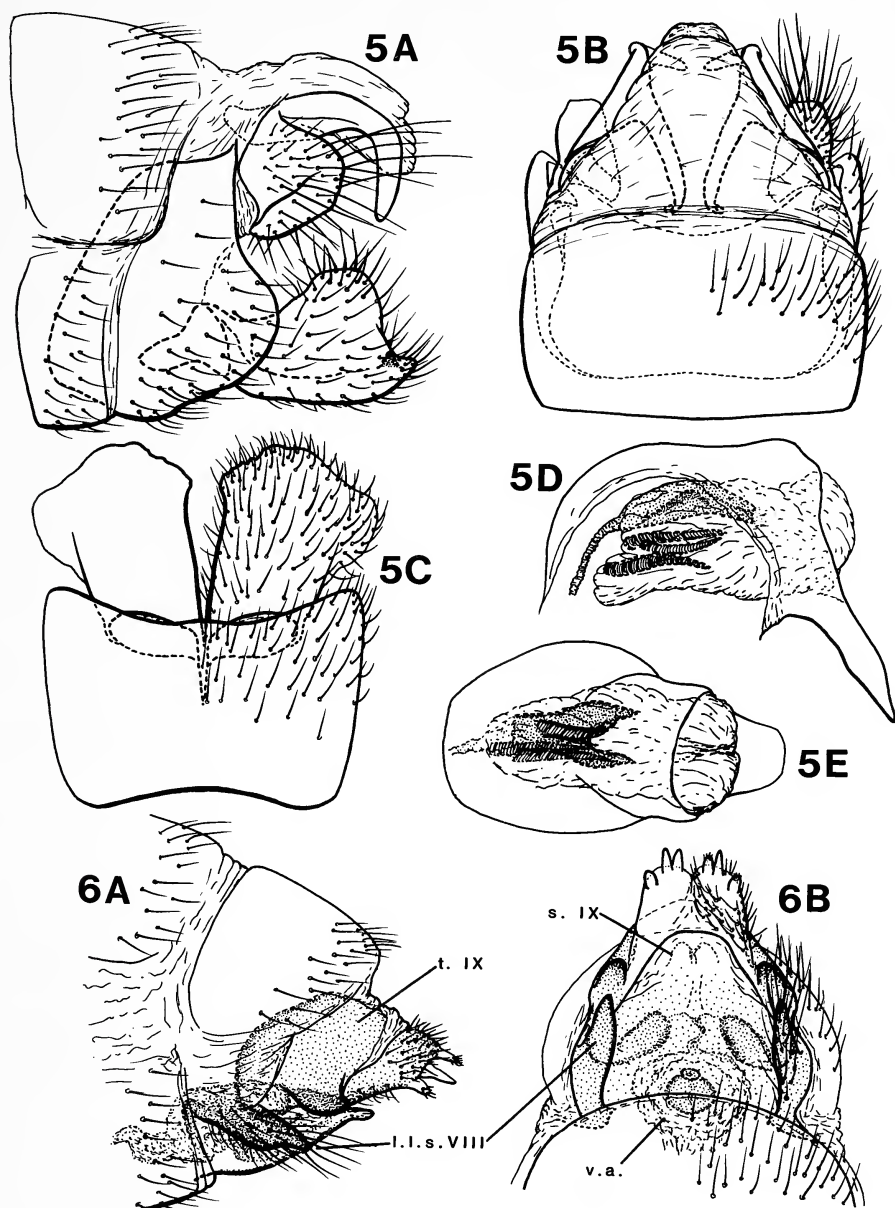
Fig. 3.   *Polycentropus fasthi.* Male genitalia: A, left lateral; B, dorsal; C, ventral; D, phallus, left lateral; E, phallus, dorsal. (inf. app. = inferior appendage, int. app. = intermediate appendage, mv. pr. = mesoventral process, ph. scl. = phallic sclerite, ph. sp. = phallic spine, pr. app. = preanal appendage, s. VIII = sternite VIII, s. IX = sternite IX, subph. scl. = subphallic sclerite, t. VIII = tergite VIII, t. IX & X = tergites IX & X).

de la Vieja, Río Negro, 10.765°N, 85.313°W, 810 m, 3.iii.1986, Holzenthal and Fasth (NMNH). Paratypes: same data as holotype, 3 males (MNCR, UMSP); Costa Rica: Alajuela: Parque Nacional Rincón de la Vieja, Quebrada Provisión, 10.769°N, 85.281°W, el. 810 m, 4.iii.1986, Holzenthal and Fasth, 1 male (UMSP); Reserva Forestal San Ramón, Río San Lorencito and tribs., 10.216°N, 84.607°W, 980 m, Holzenthal, Hamilton, Heyn, 2 males (UMSP); Cerro Campana, Río Bochinche trib., 6 km (air) NW Dos Ríos, 10.945°N, 85.413°W, 600 m, Holzenthal, Morse, Clausen, 4 males (MNCR, UMSP); Cartago: Río Platanillo, 2.2 km E Tayutic, 9.82°N, 83.55°W, 730 m, 30.i.1986, Holzenthal, Morse, Fasth, 1 male, 8 females (UMSP); San José: Parque Nacional Braulio Carrillo, Estación Carrillo, Quebrada Sanguijuela, 10.160°N, 83.963°W, 800 m, Holzenthal, Hamilton, Heyn, 4 males (UMSP).

Etymology. Named in honor of Mr. William P. Fasth, in recognition of his invaluable assistance in collecting this species and many other interesting Costa Rican Trichoptera.

Polycentropus fortispinus, new species
Fig. 4

Diagnosis. This species, a member of the *bonus* complex of the *gertschi* group, is very closely related to *Polycentropus* n. sp. 10 from near Ocosingo, Chiapas, Mexico (Hamilton, 1986, fig. 6.24). *Polycentropus fortispinus* can be separated from *P.* n. sp. 10 by rather subtle differences in the male genitalia. The bodies of the preanal appendages of the new species are larger relative to the inferior appendages; in *P.* n. sp. 10 these appendages are approximately equal in size. The larger size and more dorsal position of the mesoventral processes of the preanal appendages and the slightly larger intermediate appendages of the new species can be used to separate the two species. Also, the inferior appendages of *P. fortispinus* are less ovoid and more angular than in *P.* n. sp. 10. Finally, the numerous phallic spines are much shorter and stouter in this species than in *P.* n. sp. 10.

Description. Male: Forewing length 5.5–6.4 mm. Body sclerites and setae generally pale brown dorsally, yellow ventrally; legs with darker setae on femora and tarsi; dorsum of head brown with long, erect, dark brown setae; forewings covered with fine, dark brown setae and with numerous small, scattered patches of golden setae; forewing bases with long, erect, dark setae. Genitalia as in Figure 4. Abdominal sternite IX large, about ⅗ height of abdominal segment VIII; in lateral view approximately circular; in ventral view very broad, lateral margins and corners rounded, anterior and posterior margins shallowly concave. Intermediate appendages thin, short, not reaching length of preanal appendages; broadened at bases to form weakly sclerotized plates below tergum X; each with single seta at apex. Preanal appendages large, irregularly oval in lateral view, about ⅓ height of abdominal segment VIII, caudoventral edges concave; mesoventral processes rodlike, thicker than intermediate appendages, originating at anteroventral corners of preanal appendages, slightly longer than body of each preanal appendage. Inferior appendages short, small; in lateral view, approximately ovoid, posterior margins nearly straight; mesal teeth broad, heavy; in ventral view, posterior margins nearly straight to slightly concave, mesal margins straight, lateral margins convex. Phallus with posterior portion of phallobase short, anterior portion slightly elongate, apicoventral process broad at base, evenly decurved and narrowed to small, weakly sclerotized point; 13 short, stout phallic spines; phallic sclerite large, apical forks separated mesally; subphallic sclerite broad, extending between preanal appendages, two dorsal arms extended to encircle phallobase.

Type material. Holotype: Male, Costa Rica: Guanacaste: Parque Nacional Rincón de la Vieja, Río Negro, 10.765°N, 85.313°W, 3.iii.1986, 810 m, Holzenthal and Fasth (NMNH). Paratypes: Costa Rica: Alajuela: Reserva Forestal San Ramón, Río San Lorencito and tribs., 10.216°N, 84.607°W, 980 m, 2–4.vii.1986, Holzenthal, Heyn, Armitage, 1 male (MNCR); same, except 30.iii–1.iv.1987, Holzenthal, Hamilton, Heyn, 1 male (UMSP); Guanacaste: Parque Nacional Guanacaste, Río San Josecito [Estación Biológica Mengo], 10.992°N, 85.470°W, 960 m, 3–4.iv.1987, Holzenthal, Hamilton, Heyn, 1 male (UMSP).

*Etymology.* Named for the short, stout phallic spines characteristic of this species.

Fig. 4. *Polycentropus fortispinus.* Male genitalia: A, left lateral; B, dorsal, C, ventral; D, phallus, left lateral; E, phallus, dorsal; F, inferior appendages, caudal; G, subphallic sclerite, caudal.

Polycentropus nebulosus, new species
Figs. 5, 6

Diagnosis. This species is closest to *P. fortunus* Flint and is another member of the *bartolus* complex of the *gertschi* species group. In addition to the overall difference in shape of the inferior appendages, the presence of three phallic spines, the shorter, thicker intermediate appendages, and the absence of mesobasal spines on the inferior appendages render this species distinct from *P. fortunus.*

Description. Male: Forewing length 6.9–7.0 mm. Body sclerites and setae generally

Figs. 5, 6.   *Polycentropus nebulosus.* Fig. 5, male genitalia: A, left lateral; B, dorsal; C, ventral; D, phallus, left lateral; E, phallus, dorsal. Fig. 6, female genitalia: A, left lateral; B, ventral. (l. l. s. VIII = lateral lobe of sternite VIII, s. IX = sternite IX, t. IX = tergite IX; v. a. = vaginal apparatus).

pale brown to yellow; legs, especially femora and tarsi, with fine, dark brown setae; dorsum of head and thorax dark brown with long, erect, golden-brown setae; fore-wings covered with fine, brown setae and with scattered patches and mottled areas of golden and brown setae (Monteverde paratypes with forewings more mottled than holotype); forewing bases with long, erect, golden-brown setae. Genitalia as in Figure 5. Abdominal sternite IX large, about ¾ height of abdominal segment VIII; in lateral view, posteromesal corner rounded, produced, posterodorsal margin straight; in ventral view anterior and posterior margins broadly emarginate. Intermediate append-ages relatively thick, curved ventrad at mid-length, apices curved mesad; in length, not exceeding inferior appendages (Monteverde paratypes with intermediate ap-pendages somewhat shorter and less curved than holotype). Preanal appendages semicircular, mesoventral processes absent. Inferior appendages moderately short; in lateral view, approximately triangular, ventral margins nearly straight, with pos-teroventral corners angulate, bearing mesal point; dorsolateral flange evenly rounded; in ventral view moderately broad, mesal margin nearly straight, posterior margin irregular, dorsolateral flange slightly produced, rounded. Phallus with moderately short phallobase, apicoventral process broad basally, apex strongly narrowed; three large phallic spines (one Monteverde paratype with five phallic spines); phallic sclerite broad; subphallic sclerite weakly developed.

Female: Forewing length 8.6–10.9 mm. Color and setation as in male. Genitalia as in Figure 6. Lateral lobes of sternite VIII narrow, acute. Sternite IX trapezoidal in ventral view, posterior margin truncate, lightly sclerotized basally; densely covered with minute, fine setae. Tergite IX weakly sclerotized dorsally; with ventrolateral, round lobe. Vaginal apparatus with vase-like anterior sclerite bearing lipped central pore; pair of sclerotized pockets posteriorly.

Type material. Holotype: Male, Costa Rica: Puntarenas: Río Bellavista, ca. 1.5 km NW Las Alturas, 8.951°N, 82.846°W, 15–17.vi.1986, 1,400 m, Holzenthal, Heyn, Armitage (NMNH). Paratypes: same data as holotype except 8–9.iv.1987, Holzen-thal, Hamilton, Heyn, 2 males (UMSP); Costa Rica: Guanacaste: Parque Nacional Guanacaste, Río San Josecito, Estación Mengo, 10.922°N, 85.470°W, 28–29.vii.1987, 960 m, Holzenthal, Morse, Clausen, 3 males (UMSP); Puntarenas: Reserva Bosque Nubosa Monteverde, Quebrada Cuecha, 10.31°N, 84.79°W, 28.ii.1986, 1,500 m, Holzenthal and Fasth, 2 males, 2 females (MNCR, UMSP).

Etymology. From the Latin *nebulosus,* misty, foggy, cloudy; in reference to the often fog shrouded lower montane habitat of the species.

Polycentropus volcanus, new species
Fig. 7

Diagnosis. This species is clearly a member of the *halidus* complex of the *gertschi* group. It resembles *P. guatemalensis* Flint, *P. halidus* Milne, and *P. palmitus* Flint in the thick, moderately long intermediate appendages, the short, broad preanal appendages, the elongate inferior appendages, and the short phallus with its two phallic spines and broad phallic sclerite. It can be distinguished from those species by the ventrally directed point on the mesoventral process of the preanal appendage and by the narrow upturned apical region of the inferior appendage.

Description. Male: Forewing length 6.8 mm. Body sclerites and setae generally
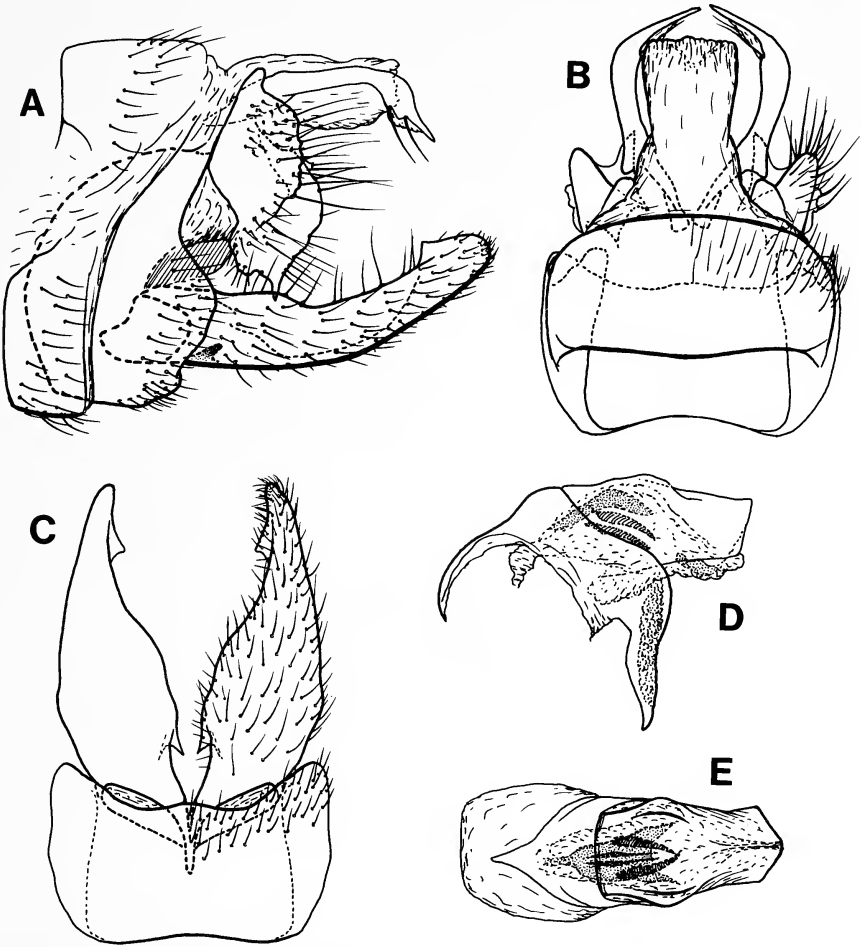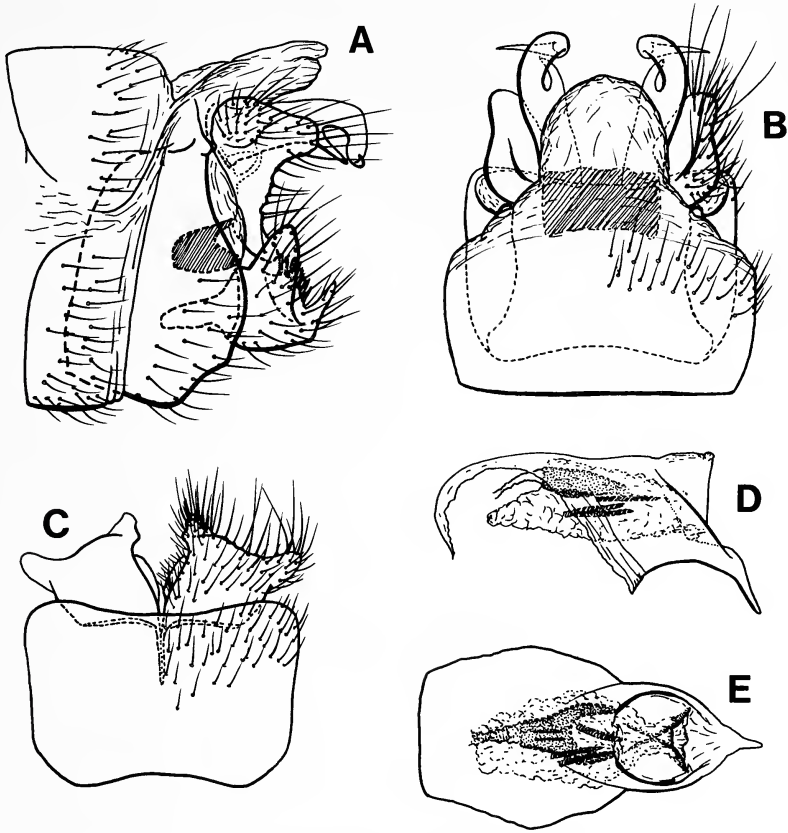
Fig. 7. *Polycentropus volcanus.* Male genitalia: A, left lateral; B, dorsal; C, ventral; D, phallus, left lateral; E, phallus, dorsal.

brownish-yellow; dorsum of head and thorax dark brown, with long, erect, dark brown setae; leg segments with dark apical setae; forewings covered with fine, brown setae and with numerous small, scattered patches of golden setae; forewing bases bearing long, erect, dark setae. Genitalia as in Figure 7. Abdominal sternite IX large, about ⅔ height of abdominal segment VIII; in lateral view, approximately hemispherical, anterior margin evenly curved, posterior margin sinuate. Intermediate appendages moderately long, but not extending posteriorly beyond inferior appendages, apical ⅓ thickened and curved ventromesally, apicomesal surfaces membranous, each with two apicoventral setae. Preanal appendages short, broad; mesoventral processes with prominent, ventrally directed, acute projections. Inferior appendages elongate, slightly upcurved, apical halves acute in ventral view; each with prominent

apicodorsal and basomesal spine-like processes. Phallus with short phallobase divided into basal and apical portions; basal portion with thick, ventrally directed apicoventral process, bearing prominent rugosity on posterior surface; apical portion simple, truncate, somewhat laterally compressed; two phallic spines; in dorsal view, phallic sclerite large, apical forks directed laterally.

Type material. Holotype: Male, Costa Rica: San José: Parque Nacional Braulio Carrillo, 6.2 km NE administration building [Estación Zurquí], 1,100 m, 10.09°N, 83.97°W, 6.ii.1986, Holzenthal and Morse (NMNH). Paratypes: San José: Río Parrita Chiquito, rt. 12, 6.5 km SW jct. rt. 2, 9.703°N, 83.970°W, 1,990 m, Holzenthal, Hamilton, Heyn, 2 males (MNCR, UMSP).

Etymology. Named for Volcán Barva near the type locality, in Costa Rica's large, highly dissected, volcanic Cordillera Central.

Polycentropus zurqui, new species
Fig. 8

Diagnosis. This species appears to be related to *Polycentropus spicatus* Yamamoto, an unplaced species within the *gertschi* group, in that the inferior appendages bear narrow, erect dorsolateral flanges and the intermediate appendages have secondary spines and laterally directed apices. The unique overall shape of these appendages on the new species distinguishes it from *P. spicatus* and all other Neotropical *Polycentropus* species.

Description. Male: forewing length 8.2–8.8 mm. Body sclerites and setae generally yellow, dark brown setae on femora and tarsi of all legs; dorsum of head and thorax brown with long, erect, dark brown setae; forewings covered with fine, brown setae and numerous, small, scattered patches of golden setae; forewing bases with long, erect, dark setae. Genitalia as in Figure 8. Abdominal sternite IX large, about ¾ height of abdominal segment VIII; in lateral view, anterior margin nearly straight, posterior margin moderately sinuate; in ventral view rectangular, nearly as long as wide, anterior and posterior margins concave. Intermediate appendages thick basally, with acute ventromesal processes, each with main body twisted, first mesally, then ventrally, then laterally; apex very acute. Preanal appendages small, slightly narrowed and rounded posteriorly; mesoventral processes thick, curved slightly posteriorly, apices rounded, blunt. Inferior appendages short, each with prominent, acute, apical tooth and erect, narrow dorsolateral flange, mesal ridges with numerous spine-like setae. Phallus with moderately short phallobase and narrow, posteroventrally directed apex; in dorsal view, phallic sclerite narrow basally, broad and U-shaped apically; three phallic spines; subphallic sclerite rectangular in dorsal view.

Type material. Holotype: Male, Costa Rica: San José: Parque Nacional Braulio Carrillo, park headquarters [Estación Zurquí], 10.059°N, 84.017°W, 1,650 m, Holzenthal (NMNH). Paratype: Same data as holotype, 1 male (UMSP).

Etymology. Named for the Río Zurquí, whose headwaters originate in pristine montane rainforest near Estación Zurquí in Costa Rica's Braulio Carrillo National Park (Fig. 1).

The following list presents new distribution records for previously described Costa Rican *Polycentropus*. Previously published distributional data for these species were presented by Hamilton (1986). *Polycentropus fortunus, P. digitus,* and *P. mayanus* are here recorded from Costa Rica for the first time. Those species preceded by an

Fig. 8. *Polycentropus zurqui.* Male genitalia: A, left lateral; B, dorsal; C, ventral; D, phallus, left lateral; E, phallus, dorsal.

asterisk (*) have been reported from the Cordillera de Talamanca of Panama and are expected to occur in the Costa Rican portion of that mountain range.

*Polycentropus acanthogaster Flint, 1981:157, figs. 46–49, male (NMNH); Hamilton, 1986:112, fig. 6.25, male.
Distribution. PANAMA (Chiriquí).

Polycentropus altmani Yamamoto, 1967:130, fig. 2, male (INHS); Flint, 1967:8, figs. 27–28 (as *P. macrostylus*); Hamilton, 1986:123, fig. 6.32, male.

New record. Costa Rica: Guanacaste: Parque Nacional Santa Rosa, Río Cuajiniquil, 10.881°N, 85.613°W, 25.vii.1987, 250 m, Holzenthal, Morse, Clausen, 1 male.
Distribution. COSTA RICA (Guanacaste, Puntarenas); ECUADOR (Pastaza); HONDURAS; NICARAGUA; PANAMA (Canal Zone, Cocle); VENEZUELA (Aragua, Lara).

Notes. The type of *P. macrostylus* Flint is from Golfito, Puntarenas Prov. This widespread species occurs at much lower elevations than other Costa Rican *Polycentropus.*

Polycentropus costaricensis Flint, 1967:8, figs. 29–32, male (NMNH); Hamilton 1986: 143.
  New records. San José: Parque Nacional Braulio Carrillo, Río Zurquí, 10.059°N, 84.019°W, 1,650 m, Holzenthal, Heyn, Armitage, 1 male.
  Distribution: COSTA RICA (Alajuela, Cartago, San José).
  Notes. This rare species is known only from the type series (male holotype, Volcán Poás; 2 male, 6 female paratypes, Volcán Irazú) and the specimen listed above from the Río Zurquí, near Volcán Barva. Flint (pers. comm.) considers this species to be synonymous with *P. spicatus* and this opinion was accepted by Hamilton (1986). However, there are distinct morphological differences between the two species, especially in the shapes of the preanal and inferior appendages. Furthermore, *P. costaricensis* is known only from the higher elevations of the volcanic peaks of the Cordillera Central, while *P. spicatus* appears to be restricted to the upper elevations of the northern Talamancas; the two populations being separated by the low elevations of the Río Reventazón valley. Unfortunately, both species are known from only a very few individuals thus limiting knowledge of intraspecific variation. We conclude that it is better to retain the separate identities of these species to call attention to the problem and hope that additional collecting will yield more specimens.

Polycentropus dentoides Yamamoto, 1967:132, fig. 6, male (INHS); Hamilton, 1986: 106, fig. 6.20, male (recorded from Costa Rica, but no specific locality information given).
  Distribution. PANAMA (Canal Zone, Chiriquí); COSTA RICA.

Polycentropus digitus Yamamoto, 1967:131–132, fig. 5, male (INHS); Hamilton, 1986:115, fig. 6.28, male.
  New records. Cartago: Reserva Tapantí, Río Grande de Orosi, 9.686°N, 83.756°W, 1,650 m, 8–9.vii.1986, Holzenthal, Heyn, Armitage, 1 male; same, except 18–21.iii.1987, Holzenthal, Hamilton, Heyn, 8 males; Puntarenas: Río Bellavista, ca. 1.5 km NW Las Alturas, 8.951°N, 82.846°W, 1,400 m, 18.ii.1986, Holzenthal, Morse, Fasth, 2 males, 2 females; San José: Parque Nacional Braulio Carrillo, Río Zurquí, 10.059°N, 84.019°W, 1,650 m, 5.ii.1986, Morse and Fasth, 1 male; same, except park headquarters [Estación Zurquí], 10.059°N, 84.017°W, Holzenthal, 1 male; same, except 7.vii.1987, Holzenthal, Heyn, Armitage, 2 males; same, except 6.2 km NE adm. build. [Estación Zurquí], 10.09°N, 83.97°W, 1,100 m, 6.ii.1986, Holzenthal and Morse, 1 male; Río Chirripó Pacífico, 9.5 km NE Rivas, 9.470°N, 83.591°W, 23.ii.1986, Holzenthal, Morse, Fasth, 16 males, 8 females.
  Distribution. COSTA RICA (Cartago, Puntarenas, San José); PANAMA (Chiriquí).

Polycentropus fortunus Flint, 1981:155, 157, figs. 42–45, male (NMNH); Hamilton, 1986:108, fig. 6.22, male.
  New records. Alajuela: Río La Paz Pequeña, 7.8 km N Vara Blanca, 10.211°N, 84.116°W, 1,230 m, 13.ii.1986, Holzenthal, Morse, Fasth, 1 male; San José: Parque Nacional Braulio Carrillo, 6.2 km NE adm. build. [Estación Zurquí], 10.09°N, 83.97°W,

1,100 m, 6.ii.1986, Holzenthal, Morse, Fasth, 2 males, 1 female; same, except park headquarters [Estación Zurquí], 10.059°N, 84.017°W, 1,650 m, 5.ii.1986, Holzenthal, 7 males, 4 females.

Distribution. COSTA RICA (Alajuela, San José); PANAMA (Chiriquí).

*Polycentropus lingulatus Flint, 1981:151, figs. 13–16, male (NMNH); Hamilton, 1986:135, fig. 6.41, male.

Distribution. PANAMA (Chiriquí, Cocle).

Polycentropus mayanus Flint, 1981:151, figs. 9–12, male (NMNH); Hamilton, 1986: 109, fig. 6.23, male.

New record. Guanacaste: Parque Nacional Guanacaste [Estación] Maritza, Río Tempisquito, 10.958°N, 85.497°W, 550 m, 19–20.vii.1987, Holzenthal, Morse, Clausen, 4 males, 1 female.

Distribution. COSTA RICA (Guanacaste); MEXICO (Chiapas).

Notes. The specimens from Guanacaste have much more pronounced apicomesal teeth on the inferior appendages compared to the holotype from Chiapas, Mexico.

Polycentropus spicatus Yamamoto, 1967:131, fig. 4, male (INHS); Hamilton, 1986: 143, fig. 6.47, male.

New records. Cartago: Reserva Tapantí, Río Grande de Orosi, 9.686°N, 83.756°W, 1,650 m, 9–8.vii.1986, Holzenthal, Heyn, Armitage, 1 male; same, except 18–21.iii.1987, Holzenthal, Hamilton, Heyn, 1 male; same, except 15–16.vii.1987, Holzenthal, Morse, Clausen, 3 males; San José: Río Parrita Chiquito, rt. 12, 6.5 km SW jct. rt. 2, 9.703°N, 83.970°W, 1,990 m, 18.vi.1986, Holzenthal, Heyn, Armitage, 2 males; same, except 10.iv.1987, Holzenthal, Hamilton, Heyn, 3 males, 2 females.

Distribution. COSTA RICA (Cartago, San José); PANAMA (Chiriquí).

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TAXONOMIC STATUS OF *KORSCHELTELLUS* BÖRNER IN NORTH AMERICA (LEPIDOPTERA: HEPIALIDAE)

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Abstract.—*Hepialus gracilis* Grote [1865], is transferred to the genus *Korscheltellus* Börner, 1925, a palearctic genus previously unrecognized from North America. *Hepialus furcatus* Grote, 1883, *H. mustelinus* Packard [1865], and *H. labradoriensis* Packard [1865], are synonymized under *Korscheltellus gracilis*. *K. gracilis* is redescribed, illustrated and its distribution and biology reviewed. The interception in Florida of a related species *K. fusconebulosus* (De Geer, 1778) is noted.

Hepialids are represented in the Nearctic Region by four genera: *Gazoryctra* Hübner [1820]; *Korscheltellus* Börner, 1925; *Sthenopis* Packard [1865]; and a fourth undescribed genus which includes members of the *californicus* species group (Wagner, 1985). The first two genera are circumpolar, although no species common to both North America and Eurasia has been recognized. *Gazoryctra* contains ten nearctic species and three palearctic species (Viette, 1949, 1953; Wagner and Tindale, in press). *Korscheltellus* contains a single North American species and several Eurasian species (Viette, 1949, 1958). The four *Sthenopis* species are confined to montane areas and the higher latitudes of North America (Forbes, 1923; Wagner and Nielsen, in prep.); the palearctic hepialids formerly placed in *Sthenopis* represent a related, undescribed genus which is currently being revised by Nielsen and Wagner (in prep.). The three species of the *californicus* group are restricted to western North America and appear to form the sister group of the palearctic *Phymatopus hecta* (Linnaeus, 1758) (Wagner, 1985).

Adults of *Korscheltellus* are dark or gray-scaled moths with mottled forewings; forewing lengths range from 12–20 mm. Characters which serve to distinguish *Korscheltellus* from other Hepialidae include the reduced, two-segmented labial palpus; a protibial epiphysis; a weakly developed vein Scl; the absence of a metatibial androconial hairpencil; and in the male genitalia, the anteromedially inflected tegumen and the elongate and simple valva (without a basal lobe or strongly melanized spines).

The four named North American *Korscheltellus* were originally described in the genus *Hepialus* Fabricius, 1775: *gracilis* Grote [1865]; *labradoriensis* Packard [1865]; *mustelinus* Packard [1865]; and *furcatus* Grote, 1883. All are treated here as conspecific. The first three species were described in the same number of volume three (1864) of the Proceedings of the Entomological Society of Philadelphia, which appeared in March of 1865 (Brown, 1964). Although *mustelinus* has page precedence, *gracilis* is the more widely used name and its type is still extant, and therefore, it is held to be the valid name.

Korscheltellus gracilis recently has been implicated as a forest pest in New England and is targeted for intensive study by the United States Forest Service. This paper is meant to review the taxonomy of the group and summarize existing distributional

and biological data. *Korscheltellus gracilis* is redescribed below. Characters known to vary within the genus and in related palearctic taxa are emphasized. Genital nomenclature follows Birket-Smith (1974), Ueda (1978), and Nielsen and Robinson (1983); veins are named as in Nielsen and Robinson (1983); scale ultrastructural terminology follows Downey and Allyn (1975) and Kristensen (1978).

Korscheltellus gracilis Grote, **New Combination**

Hepialus gracilis Grote [1865]:522. Type Locality: Canada, Quebec. Type: female in ANSP.

Hepialus mustelinus Packard [1865]:393. Type Locality: USA, Maine, Brunswick. Type: female, lost? New Synonymy.

Hepialus labradoriensis Packard [1865]:394. Type Locality: Canada, Labrador, Salmon Bay, Caribou Island. Type: male in MCZ. New Synonymy.

Hepialus furcatus Grote, 1883:30. Type Locality: USA, New York, Adirondacks. Cotypes: three males and one female, lost? New Synonymy.

Redescription. Male (Figs. 1, 2): forewing length: 13–15 mm. Antenna with 23–28 segments. Labial palpus short, 0.15–0.18 mm, two-segmented, the distal segment reduced, sensory pit apical; apex of mentum with short membranous extension (Fig. 3). Maxilla well developed, more than 0.10 mm. Head and thorax with long tan to black trichoid scales, both light- and dark-tipped; dark scales on palpi, under eyes, and thoracic venter. Epiphysis one third length of protibia, nearly twice as long as broad, apex acute (Fig. 4). Forewing mottled with tan, fuscous, and black scales, with indistinct basal band of paler scales running from wing base to inner margin before tornus, and with oblique band from postmedian area of inner margin to apex. Venation (Fig. 5): Scl vestigial, R2+3 long-stalked, separating between 0.62–0.72 length of R3. Forewing scales at least twice as long as broad, with deeply toothed apices (Fig. 8). Secondary ridges usually distinct; fluting conspicuous; windows separated by one or two arcing transverse flutes, small, round to irregular, bordered by either ring of unmodified cuticle (Fig. 9) or raised quadrangular area (Figs. 12, 13); window membrane often present. Hindwing fuscous, patterned at apex. Fringe checkered, darker scales adjacent to veins. Abdomen tan to dark brown, anal tuft often obscure.

Male genitalia. (Fig. 6). Genital capsule approximately circular in caudal view. Anterodorsal margin of tegumen with inflection along midline; valvellar processes long, projecting caudad, strongly melanized apically, apex and ventral margin microserrulate. Mesosome tongue-like, distal half bent ventrad at ca. 45 degrees. Lateral margin of juxta constricted before caudal margin. Valva elongate, narrowed below costa, with lightly pigmented costal tooth; setose over distal half. Vinculum broadly U-shaped; saccus differentiated as a shallow ventral lobe; acrosternite triangular or rounded.

Female. (Fig. 2). Forewing length 14–19 mm. Antenna with 25–28 segments. Wings often lightly scaled; ground color pale brown, maculations diffuse, few black or white scales, oblique and basal bands often broad, confluent along inner margin.

Female genitalia. (Fig. 7). Corpus bursae ovate, extending to caudal margin of A6, nearly as long as ductus bursae. Papillae anales narrow, setose over distal half, modestly differentiated from T8 dorsad, with deep medial notch or free over midline, anterolateral portion constricted and then flared at base. Subanal plate elongate,
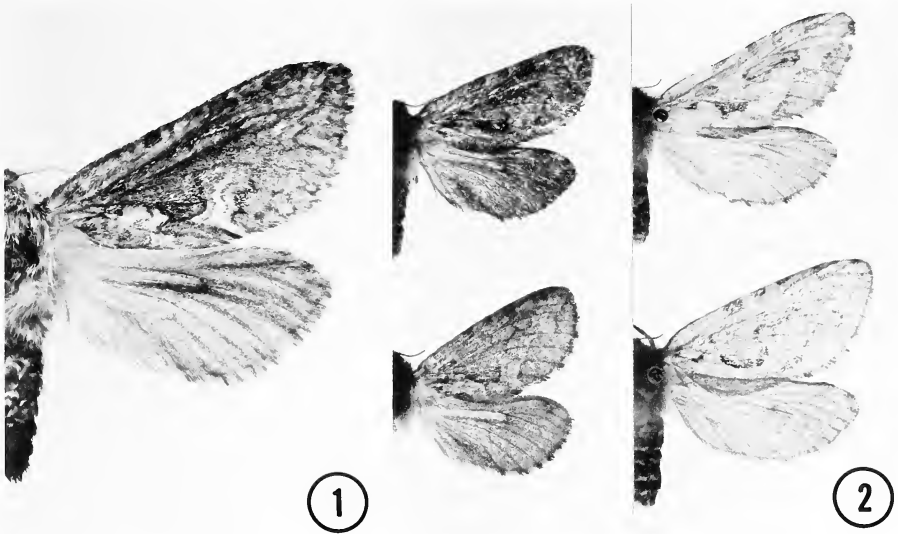
Figs. 1, 2.   *Korscheltellus gracilis* adults: 1. Male; 2. Individual variation, males on left and females on right.

obliquely quadrangular. Medial lobe 1.2–2.0× as broad as long, setose. Lateral plate weakly differentiated, setose, circa 3× as broad as long.

Diagnosis. Generic features will separate *K. gracilis* from all other nearctic swift moths: adults small, darkly mottled; epiphysis about one third length of protibia; tibial spurs absent; in males, metatibial androconial brush organs absent. The male genitalia are diagnostic: mesosome tongue-like; acrosternite prominent; valvellar processes long, horn-like, and strongly melanized.

Korscheltellus gracilis closely resembles the palearctic species *K. fusconebulosus* (De Geer, 1778). *K. fusconebulosus* tends to be larger and more strongly marked. The forewing of male *gracilis* rarely has pronounced spots of white scaling, whereas that of *fusconebulosus* often has a white spot at the base of M1 and/or a second spot over the confluence of M2 and M3 in the cell. The male of *fusconebulosus* frequently has a series of submarginal spots that are absent in *gracilis*. The valvellar processes in *gracilis* are short, curve outward apically and project venterocaudad; those of *fusconebulosus* are longer, run nearly parallel, and project downward.

Variation. Like many other hepialids, differences in color and pattern are considerable. Adults from Camels Hump, Chittenden Co., Vermont, range from light brown to nearly black. Northern specimens (e.g., Newfoundland) tend to be dark brown with obscure maculation. Males from the Great Smokies also tend to be dark. Females and older individuals are often sparsely scaled. Variation occurs in several genital structures. The costal tooth on the valva is small and rounded in some specimens, prominent and acute in most. The acrosternite can be acute or rounded. The dorsal margin of the vinculum is entire or bears a small condyle at its basal articulation with the valva. In some populations the shape of the 8th sternite is variable, ranging
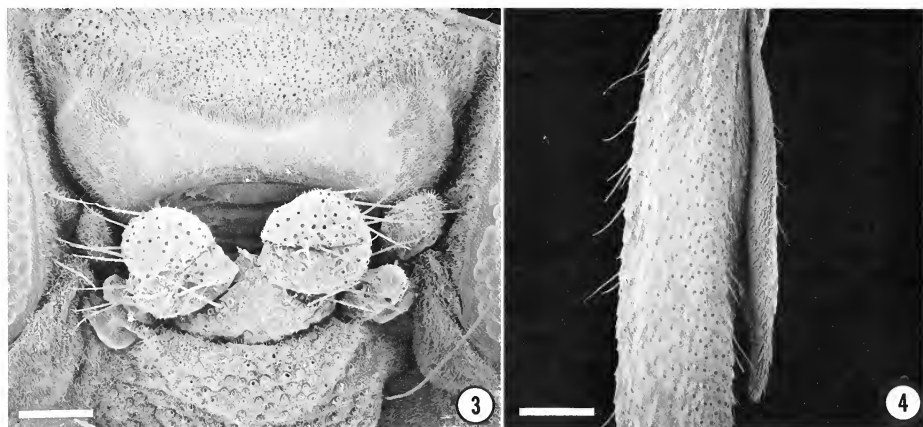
Figs. 3, 4.   Scanning electron micrographs of *Korscheltellus gracilis*: 3. Head, frontal view, scale = 200 μm; 4. Epiphysis, scale = 60 μm.

from twice as broad as long to nearly quadrangular; its posterolateral margin is entire or emarginate.

Material examined. 441 males, 83 females, and 15 unsexed specimens from eastern North America. Label data are available upon request. The primary types of *labradoriensis* (DLW Slide 86-82) and *gracilis* (DLW Slide 87-05) were examined. The female type of *mustelinus* was not with *labradoriensis* in the Packard Collection in the MCZ and is presumed lost. The types of Grote's *furcatus* were not in the ANSP with the type of *gracilis,* nor were examples found in the Buffalo, British, or American Museums of Natural History, known depositories of Grote's material (Horn and Kahle, 1935).

Distribution (Fig. 14). Labrador (to 53.5°N lat.) west to Hudson Bay, Ontario, and Edson, Alberta, south to Wisconsin and Michigan, and in the Appalachians to North Carolina. Across eastern North America, the range of *gracilis* corresponds to that of the boreal life zone.

Specimens labeled "Manchester [brown ink], Massachusetts [black ink]" from the Henry Edwards collection (in USNM, BMNH, and ANSP) appear to represent mislabeled *K. fusconebulosus.* All are larger and have more antennal segments than typical *K. gracilis*; the male genitalia agree with those of *fusconebulosus.* Perhaps these moths were collected in Manchester, England, and then inadvertently mislabeled. A specimen in the LACM labeled "Westfield, Union Co., N.J." would seem to be mislabeled. Forbes' (1923) reference to *gracilis* from Colorado is almost certainly in error, and probably refers to *Hepialus hectoides* Boisduval, 1868.

Remarks. Neither Packard nor Grote examined venation or prepared dissections. The original descriptions of *furcatus, gracilis, labradoriensis,* and *mustelinus* addressed only superficial differences in wing pattern (such characters are highly variable in the Hepialidae as in many other nocturnal Lepidoptera). Phenotypic variation in large series exceeds that presented in the four descriptions by Packard and Grote. A specimen of *Korscheltellus gracilis* from Hudson Bay, Canada, in the BMNH, is labeled with a manuscript name, *Hepialus griseus.*
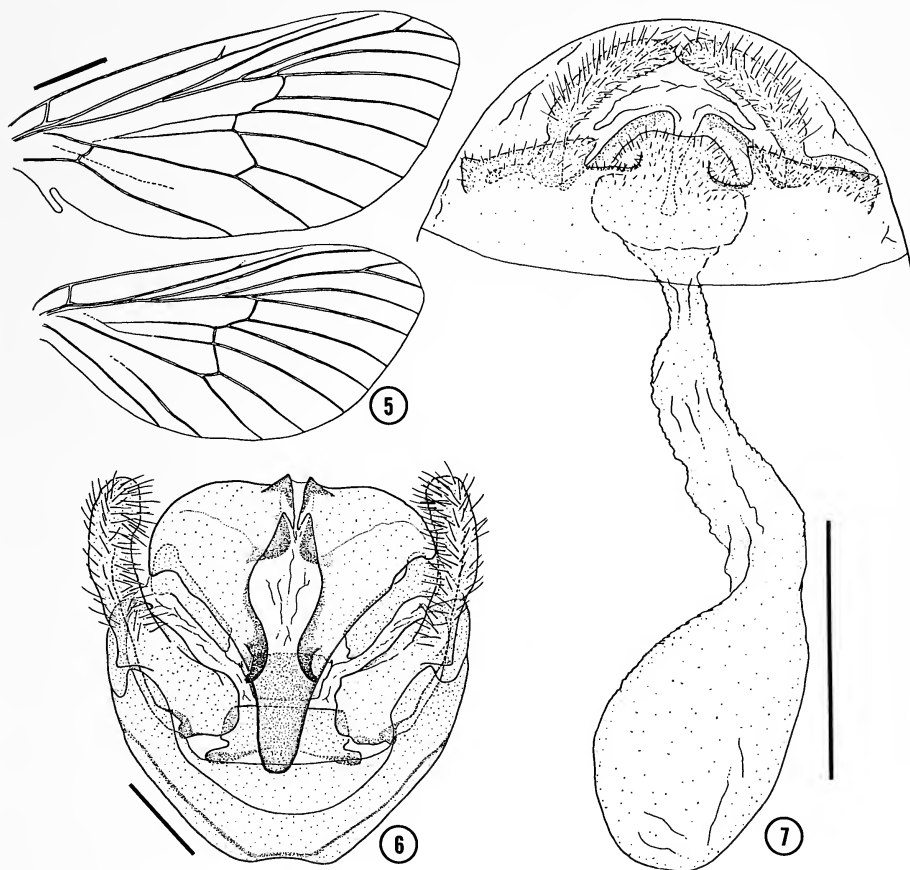
Figs. 5–7. *Korscheltellus gracilis*: 5. Wings, scale bar = 2.0 mm; 6. Male genitalia, caudal view, scale bar = 0.25 mm; 7. Female genitalia, ventral view, scale bar = 1.0 mm.

BIOLOGY

The small, shiny black, ovoid eggs are smooth with indistinct micropyles. One female can lay a few hundred eggs which hatch after one or two weeks (Packard, 1895).

The larva is a subterranean polyphage feeding on roots externally or boring into below-ground tissues. Felt (1906) recorded larvae of *Korscheltellus gracilis* in association with the roots of spruce (*Picea* Dietr.). Packard (1895) found moths common in stands of red spruce (*Picea rubens* Sarg.) in Brunswick, Maine, and assumed this to be the larval foodplant. In Canada the larvae have been associated with the roots of white spruce (*Picea glauca* Voss), balsam fir (*Abies balsamea* Mill.), and yellow birch (*Betula lutea* Michx.) (Prentice, 1965). D. Tobi (pers. comm.) found larvae in association with below-ground portions of red spruce, balsam fir, paper birch (*Betula papyrifera* var. *cordifolia* Fern.), and the fern, *Dryopteris campyloptera* Clarkson.

Korscheltellus gracilis has a two-year life cycle over much of its range. Although adults fly every year at a given locality, years of abundance alternate with poor ones. Large series of adults have been collected at four localities over a span of three or more years: at Lake Katherine, Oneida Co., Wisconsin, from 1945–1963 by H. M. Bower; at [St.-Theodore-de-] Chertsey, Quebec, from 1966–1969 by L. Le Sage; in southern Nova Scotia, from 1957–1979 by D. C. Ferguson and B. Wright; and on Camels Hump, near Huntingdon, Chittenden Co., Vermont, from 1984–1986 by D. Tobi. At Lake Katherine and in Nova Scotia most adults have been captured in odd-numbered years, with only occasional records for even-numbered years. At Camels Hump and Chertsey, most captures have been made in even-numbered years.

The adults fly at dusk from the end of June until the middle of August with the majority of records falling between mid-July and early August. The males are strong, erratic fliers, careering among trees and underbrush in search of females (Engelhardt, 1920). Adults are attracted to light.

Korscheltellus gracilis is principally an inhabitant of coniferous forests. It is especially common in stands where red spruce and balsam fir are dominants (D. Tobi, pers. comm.). In the southern Appalachians *gracilis* is a high elevation species, but in Maine, Nova Scotia, and northward, colonies may occur at sea level.

DISCUSSION

Fabricius created the genus *Hepialus* for *Phalaena* (*Noctua*) *humuli* L. in 1775. Since that time the genus *Hepialus* has been used by lepidopterists worldwide for small, nondescript Hepialidae, whereas large colorful or otherwise distinctive species have been placed in other genera. However, several characters indicate that *Hepialus humuli* and the members of the holarctic genus *Sthenopis* (with *Zenophassus* Tindale, 1941, *Aenetus* Walker, 1856, and perhaps others), share a common ancestor not shared by many "*Hepialus*" species. Synapomorphies for the two taxa include (1) metatibial hairpencils in males, (2) swollen metatibiae in males,[1] (3) triangular forewings with falcate apices, (4) forewing scales with rounded apices, and (5) the absence of an epiphysis in all but *Aenetus*. Hence if *Sthenopis* is to be retained as a distinct genus, as has been done by all lepidopterists since the genus was first described by Packard in 1865, then more distantly related "*Hepialus*" species are properly classified in other genera.

The generic placement of *gracilis* is problematical. The Eurasian *fusconebulosus* appears to be the most closely related hepialid to *gracilis*. Some individuals of the two moths, especially females, are nearly indistinguishable. Taken together, they

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Figs. 8–13.   Scanning electron micrographs of forewing scales from the median area: 8. *Korscheltellus gracilis* forewing scale; 9. Ultrastructural of same, typical micromorphology; 10. *Pharmacis carna*; 11. *Korscheltellus lupulinus*; 12 and 13. *Korscheltellus gracilis* from Wisconsin and Ontario, respectively. Scale bar = 50 μm for Figure 8 and 3.0 μm for Figures 9–13.

[1] Some *Aenetus* species and members of the "*Sthenopis*" *regius* group have secondarily lost the swollen tibiae and hairpencils.
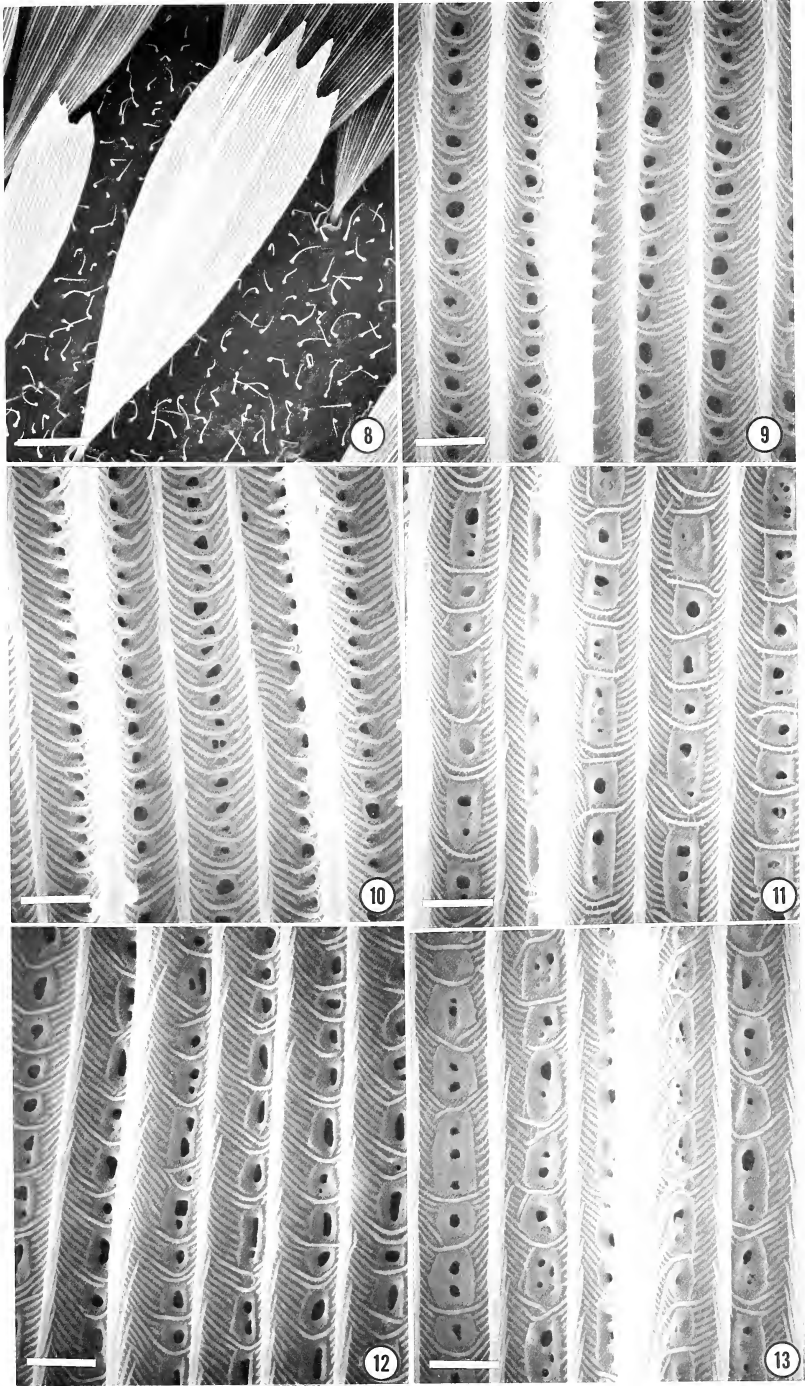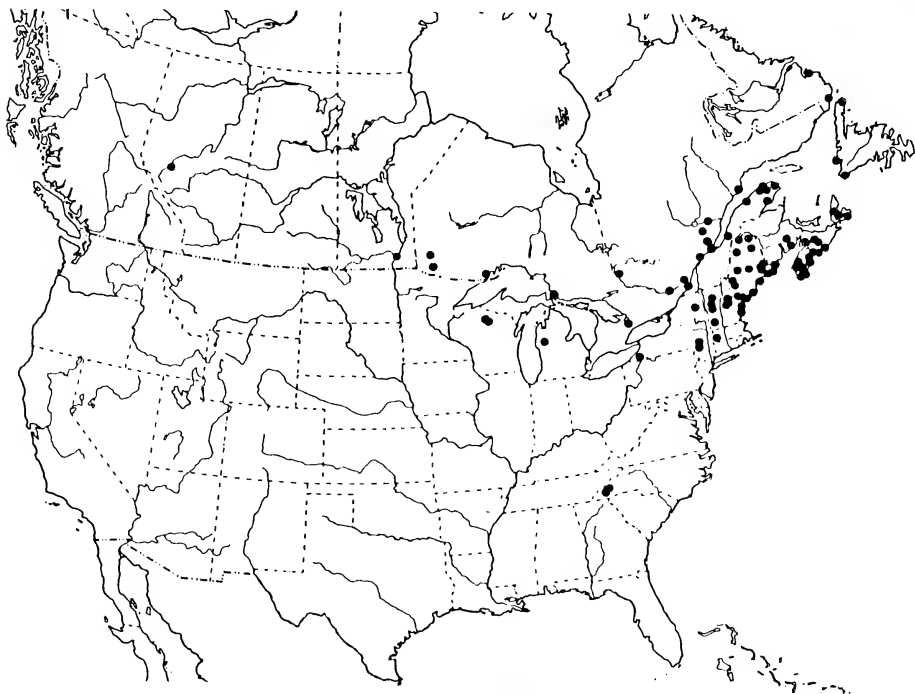
Fig. 14.   Distribution of *Korscheltellus gracilis*.

show affinities to two palearctic genera: *Korscheltellus* (type species: *lupulinus* L., 1758) and *Pharmacis* Hübner [1820] (type species: *carna* Denis and Schiffermüller, 1775). *Korscheltellus* can be characterized by male genital and wing scale ultrastructural characters; synapomorphies for *Pharmacis* have not been identified.

Viette (1948, 1949, 1958) placed *fusconebulosus* in *Korscheltellus* because of similarities in the male genitalia, but he did not describe specific structures. An examination of the male genitalia of *lupulinus* and *fusconebulosus* (along with *gracilis*) supports his view: all share simple, elongate valvae; horn-like valvellar processes; free processus momenti that lie in the same plane as, and below, the tegumen; a hat-shaped juxta, constricted before the vincular margin; a tongue-like mesosome; and a triangular or rounded, dorsally projecting acrosternite.

The forewing scale ultrastructure of *gracilis* suggests an affinity to *Pharmacis*. The scales of *Pharmacis carna* bear small circular to irregular windows surrounded by a ring of smooth cuticle; adjacent windows are separated by one or two (occasionally more) arcing transverse flutes (Fig. 10). The typical ultrastructure of *gracilis* is similar (Fig. 9). The wing scale ultrastructure of *Korscheltellus lupulinus* differs markedly from the above. The window membrane is often present, and groups of windows are surrounded by quadrangular areas of raised cuticle (Fig. 11). However, the occasional specimen of *gracilis* is intermediate, seemingly bridging these two scale types (Figs. 12, 13).

The forewing color and pattern of *Korscheltellus, Pharmacis,* and *gracilis* are gen-

erally similar. Males tend to be mottled with various brown, tan or gray scales; the markings are especially close in females. All are moderately small hepialids with forewing lengths rarely exceeding 19 mm.

As evident from the above, it is not possible to definitively assign *gracilis* to either *Korscheltellus* or *Pharmacis*. It is quite possible that *Korscheltellus* will prove to be a subordinate taxon within *Pharmacis*. For now, I follow Viette (1948, 1949, 1958), Popescu-Gorj (1979), and Inoue (1982), in placing *gracilis* with *fusconebulosus* in the genus *Korscheltellus*.

In July of 1985, a male of *Korscheltellus fusconebulosus* was intercepted in Florida by the United States Department of Agriculture. The individual was collected from an air cargo shipment that originated in Denmark.

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THE LARVA OF *NOTOSTIGMA*
(HYMENOPTERA: FORMICIDAE: FORMICINAE)

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Abstract. — The larvae of worker and sexual castes of the ant *Notostigma carazzii* from Australia are described and illustrated.

We have studied the larvae of 182 genera of ants; that leaves about a hundred genera still to be done. In our 1986 supplement (p. 697) we complained that "our stream of incoming larvae has dwindled to a mere trickle." When we complained to a young colleague that we were not getting additional genera, he replied that the genera we had "not studied were those whose nests are found only by accident . . . . So we looked up the history of the 103 genera which we have not studied: 62% have been reported only once (probably the type nest or only the type specimen), 23% we consider rare and only 15% common."

The chief purpose of the above preamble is to let the reader know how grateful we are to our Australian colleague, Dr. R. W. Taylor, for sending us 160 larvae and 6 workers of that extraordinary ant *Notostigma carazzii.*

Collection data. N. Queensland. Boar Pocket, 17°10'S, 145°39'E, in rain forest, nesting in soil, 720 m elevation. Collected by R. W. Taylor, S. Higashi and T. Matsumato.

Acknowledgment. The collecting expedition was funded by the Japanese Ministry of Science.

Caution. The reliable determination of instar, caste and sex of larvae requires the following specimens: a first-instar larva inside an egg ready to hatch; a second-instar larva inside a first-instar ready to moult; a third-instar larva inside a second-instar larva ready to moult, etc.; and finally a mature larva. Maturity is proved by a prepupa, which will reveal all characters of a mature larva except shape. For further confirmation a worker pupa or a worker is desirable to check size. If the worker caste is polymorphic, a prepupa of each size is required. Mature sexual larvae can be recognized only from prepupae ready to moult to pupae. For immature sexuals we have no rule.

From the above paragraph it follows that even with this magnificent collection of *Notostigma* larvae we cannot determine instars, castes or sex.

Genus NOTOSTIGMA Emery

Profile pogonomyrmecoid (i.e., diameter greatest near middle of abdomen, decreasing gradually toward anterior end and more rapidly toward posterior end, which is rounded; thorax more slender than abdomen and forming a neck, which is curved ventrally). Praesaepium lacking. Body hairs dense, mostly 2- to 4-branched. Head hairs numerous, mostly unbranched. Labrum deeply bilobed; chiloscleres lacking.

Mandibles camponotoid (i.e., base broad, its width at least ⅔ the length; apex forming a small short tooth; no medial teeth; medial border erose).

Notostigma carazzii (Emery)

Mature (?) worker larvae. Length (through spiracles) 8.3–15.4 mm. Profile pogonomyrmecoid; anus with a small posterior lip; gonopod vestiges on AVIII and AIX; 13 differentiated somites. Spiracles on T2 0.035 mm in diameter, decreasing slightly posteriorly. Integument on venter of anterior somites with spinules in short transverse rows. Body hairs dense (too dense to draw), the longest with flexuous tips, and uniformly distributed; of 2 types: (1) numerous, 0.1–0.35 mm long, 2- to 4-branched; (2) few, 0.13–0.3 mm long, unbranched. Cranium subhexagonal, broader than long, with bulging genae and a pair of small swellings near dorsal surface; clypeus and labrum slightly swollen anteriorly. Antennae just above midlength of cranium; with 3 sensilla mounted on a small sclerotized knob, which is seated on a large slight elevation. Head hairs numerous (about 110); 0.125–0.25 mm long; mostly unbranched, a few bifid or with bifid tip. Labrum deeply bilobed; anterior surface of each lobe with an irregular swelling bearing about 14 short hairs or spinulose sensilla; ventral surface with 4 sclerotized sensilla and with short rows of spinules medially; entire posterior spinulose dorsally and with numerous ridges arranged in rows which radiate from the dorsolateral angles and with about 14 small isolated sensilla. Mandible camponotoid; heavily sclerotized; apex short and curved medially, with numerous short sublongitudinal ridges on anterior surface; posterior surface with ridges sublongitudinal ventrally but curving to transverse at about midlength; medial border erose. Maxilla with conoidal apex, covered with short rows of minute spinules, palp paxilliform with 5 (2 apical with a spinule each and 3 lateral) sensilla; galea digitiform with 2 apical sensilla. Labium with moderately long, rather numerous rows of minute spinules medially; lateral surfaces with numerous short arcuate ridges; palp paxilliform with 5 (2 apical and with a spinule each and 3 lateral) sensilla; opening of sericteries a wide transverse slit with a recurved sclerotized bar at each end. Hypopharynx densely spinulose; the spinules arranged in subtransverse rows, the rows grouped in 2 subtriangles which have their bases near the middle, the spinules so long and the rows so close together that the spinules overlap.

Immature (?) larvae. Length (through spiracles) 8.7–10.3 mm. Similar to mature (?) larva except as follows. Body more slender. Body hairs (1) few, 0.05–0.4 mm, 2- to 4-branched; (2) numerous, 0.005–0.4 mm, unbranched. Head hairs less numerous (about 97), 0.05–0.2 mm long, unbranched, flexuous. Palp a short peg.

Young larva. Length (through spiracles) 5.4–10.2 mm. Similar to immature (?) larva except as follows. Body more slender. Integument with sparse minute spinules of AX also. Body hairs less numerous (but too dense to draw), of 2 types: (1) very few, 0.05–0.4 mm long, bifid or with bifid tip; (2) numerous, unbranched. Head hairs slightly less numerous (about 94); 0.1–0.2 mm long, with flexuous tip. Maxillary palp a skewed sclerotized knob; galea a frustum. Labium with a few short rows of minute spinules; palp a skewed frustum; opening of sericteries a short transverse slit, a pair of low knobs lateral to opening.

Very young larvae. Length (through spiracles) about 3.7 mm. Similar to young larva except as follows. Body nearly straight and of same diameter throughout; head
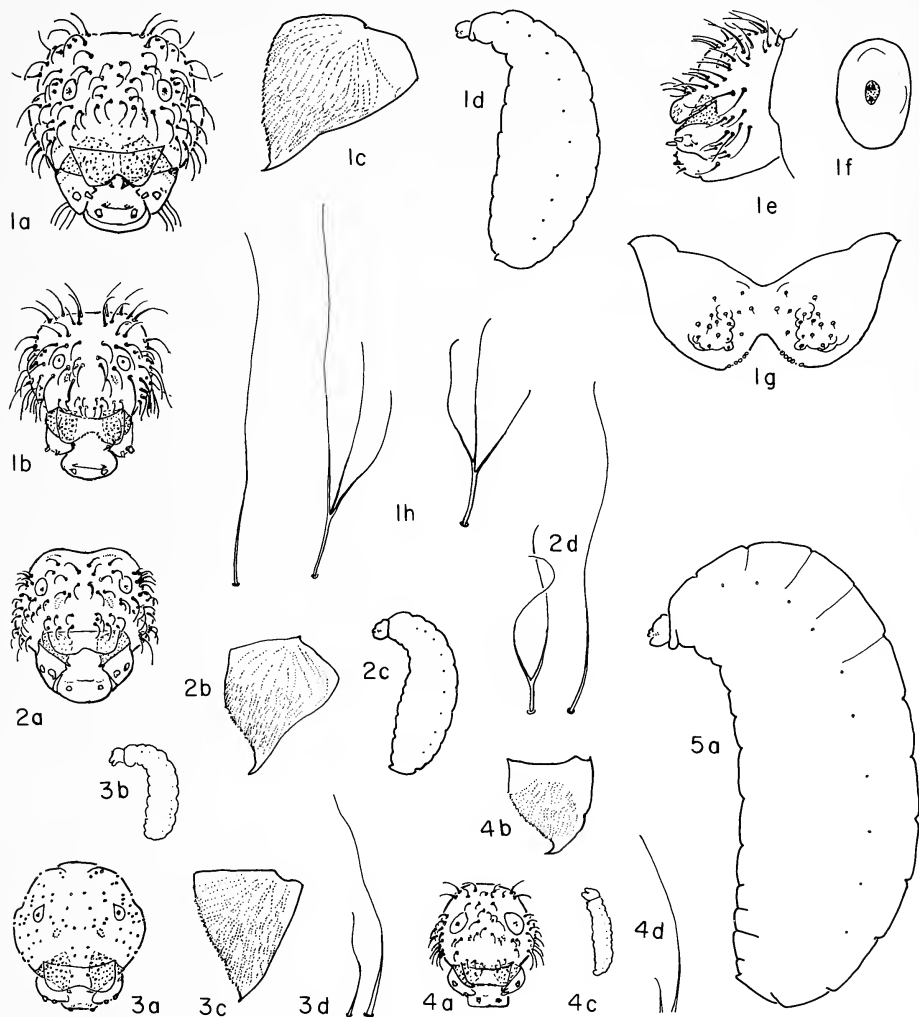
Figs. 1–5. 1. Mature (?) larva. a, Large head in anterior view, ×25; b, small head in anterior view, ×25; c, left mandible in anterior view, ×76; d, larva in side view (hairs omitted), ×3; e, head in side view, ×25; f, left antenna in anterior view, ×100; g, labrum in anterior view, ×100; h, one unbranched and 2 branched body hairs, ×100. 2. Immature worker larva. a, Head in anterior view, ×25; b, left mandible in anterior view, ×76; c, larva in side view (hairs omitted), ×3; d, 2 body hairs, ×100. 3. Young larva. a, Head in anterior view, ×25; b, larva in side view (hairs omitted), ×3; c, left mandible in anterior view, ×76; d, 2 body hairs, ×100. 4. Very young larva. a, Head in anterior view, ×25; b, left mandible in anterior view, ×100; c, larva in side view (hairs omitted), ×3; d, body hairs, ×100. 5. Sexual (?) larva. a, larva in side view (hairs omitted), ×3.

on anterior end and of about same diameter as body; anus ventral. Integument with spinules in short rows on dorsum of AVIII to AX and with a few on venter of thorax. Body hairs fewer (but too numerous to draw) on T1–T3 and AI–AIII (decreasing in number toward AIII); 0.025–0.25 mm long, the longest with flexuous tips; most unbranched, a very few bifid. Cranium with slightly bulging genae. Head hairs fewer (about 80); 0.036–0.12 mm long. Labrum feebly bilobed; each lobe with about 11 sensilla on a slight elevation, ventral surface with 5 sensilla. Maxilla with round-pointed apex bearing a few minute spinules; palp a sclerotized slight elevation; galea a sclerotized slight elevation; opening of sericteries a short transverse slit. Hypopharynx with numerous fine short ridges, which are arranged in rows radiating from dorsolateral angles.

Sexual (?) larvae. Length (through spiracles) 17–23 mm. Similar to mature (?) larva except as follows: Body hairs less numerous (but too numerous to draw); 0.2–0.3 mm long; similar to hairs on young larva but with thicker base. Of 2 types (1) most numerous, unbranched; (2) very few, bifid or bifid-tipped. Head hairs more numerous (about 116); 0.1–0.225 mm long; unbranched. Spinules on posterior surface of labrum more numerous and longer dorsally. Apex of maxilla conoidal and with numerous short rows of minute spinules. Hypopharynx with more numerous rows of longer spinules dorsally. (We suspect that these large larvae are sexual because of their size but they have the hairs of immature larvae.)

In our key to ant larvae (1976:72) the larva of *Notostigma* keys to Formicinae but not to the tribe Camponotini to which it has been assigned, because it lacks chiloscleres. Therefore it must be lumped with five inseparable tribes under 27b on p. 73.

The tribe Camponotini contains 11 genera: 8 of which we have studied (*Calomyrmex, Camponotus, Colobopsis, Dendromyrmex, Echinopla, Notostigma, Opisthopsis* and *Polyrhachis*) and 3 which we have not seen (*Forelophilus, Overbeckia* and *Phasmomyrmex*). All those studied, except *Notostigma,* possess chiloscleres and a praesaepium, which are found nowhere else among ant larvae. Furthermore the specialization index for *Notostigma* is 18, whereas the average for the other 7 is 22, with 20 as the lowest.

Can it be, therefore, that *Notostigma* is misplaced? We do not think that larval characters should get priority. But when the unique characters are found in a majority of the genera of a tribe but are lacking in one genus, the adults should be restudied.

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ON THE FIRST AFRICAN AND AUSTRALIAN SPIDERS OF THE GENUS *CYRIOCTEA* (ARANEAE: ZODARIIDAE)

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Abstract.—The spider genus *Cyrioctea,* previously known only from Chile and Argentina, is newly recorded from Namibia (*C. whartoni, C. hirsuta,* and *C. namibensis,* new species) and Queensland (*C. raveni,* new species).

Members of the remarkable spider genus *Cyrioctea* Simon (1889) are easily recognized by the presence of a transverse series of spines (six in number, except in the type species *C. spinifera* Nicolet, which has up to 10 spines) situated between the anterior and posterior eye rows (Schiapelli and Gerschman, 1942, pl. 1; Platnick, 1986, figs. 1–3). It seems likely that the cephalic spines are used primarily for burrowing into sand, as the five species described to date are known only from sand dunes and sandy inland areas in Chile and Argentina (Platnick, 1986). It was with great interest, therefore, that we independently found additional species of the genus, described below, from similarly sandy areas in Australia and southern Africa.

The familial placement and relationships of *Cyrioctea* are uncertain. Although the absence of a serrula, the elevated clypeus, the slightly reduced median and posterior spinnerets, and the genitalic conformation suggest that the genus belongs to the Zodariidae, the teeth on the tarsal claws are not confined to the inner edge of the claw as in typical zodariids (Jocqué, 1986, 1987; Platnick, 1986). It is entirely possible, therefore, that *Cyrioctea* represents the sister group of most, or all, other zodariids, and the unusually widespread distribution now documented for the genus accords well with that possibility.

With six of nine species known from only one sex, it is difficult to test any hypotheses about the interrelationships of the American, African, and Australian species. One notable character, however, is the near fusion of tarsi and metatarsi I in the known females from Africa and Australia but not America.

The format of the descriptions follows that of Platnick (1986). We thank Dr. M. U. Shadab of the American Museum of Natural History for help with illustrations, and Drs. R. J. Raven and V. E. Davies for access to the collections of, and their hospitality during the first author's visit to, the Queensland Museum. This work was partially supported by National Science Foundation grants BSR-8312611 and BSR-8406225 to the first author.

Cyrioctea whartoni, new species
Figs. 1–2

Types. Male holotype from Kuiseb River, Gobabeb, Namibia (June 15–July 20, 1979; R. Wharton), deposited in the State Museum, Windhoek (SMN 40773); paratype male (same data), deposited in the American Museum of Natural History.
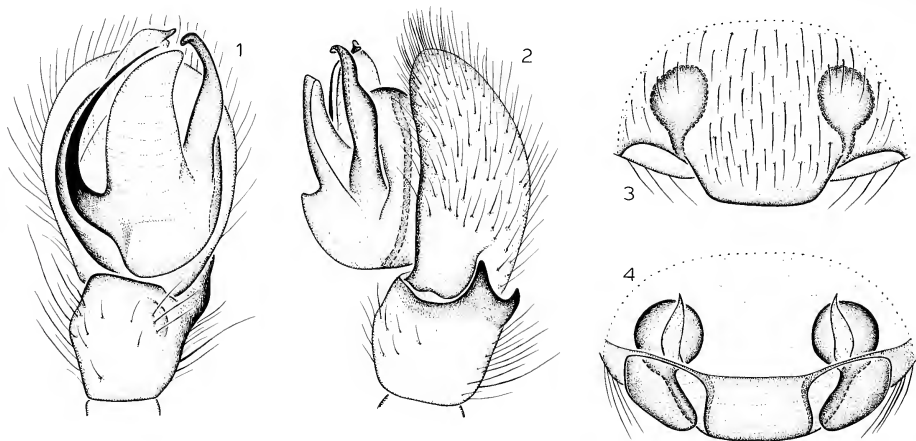
Figs. 1–4. 1. *Cyrioctea whartoni,* left male palp, ventral view. 2. Same, retrolateral view. 3. *C. hirsuta,* new species, epigynum, ventral view. 4. Same, dorsal view.

Etymology. The specific name is a patronym in honor of the collector of the types.

Diagnosis. The long narrow embolus occupying most of the prolateral side of the palpal bulb distinguishes males of this species from those of all other known *Cyrioctea.*

Male: Total length 4.01. Carapace 2.36 long, 1.67 wide. Femur II 1.60 long. Eye sizes and interdistances: AME 0.09, ALE 0.08, PME 0.08, PLE 0.10; AME-AME 0.04, AME-ALE 0.01, PME-PME, 0.07, PME-PLE 0.06, ALE-PLE 0.08; MOQ length 0.33, front width 0.22, back width 0.23. Embolus situated at prolateral edge of palpal bulb, long, spiniform (Fig. 1); retrolateral tibial apophysis bifid (Fig. 2). Leg spination: femora: I d1-2-1, p0-0-1, r0-0-1; II d2-2-1, p0-0-1, r1-1-1; III d0-1-2, p0-1-1, r1-1-1; IV d2-2-0, p0-1-1, r0-0-1; patellae: II 0-1-0; IV d0-0-1, p0-0-1; tibiae: I p0-0-1, v0-2-3; II v1r-1r-2, r0-1-1; III d1-2-1, p2-0-1, v2-2-2; IV d1-0-1, p1-0-1; metatarsi: I p0-0-0, r0-0-0; II p1-0-1, v2-1r-2, r0-0-0; III d0-0-0, p1-2-2, r1-2-1; IV d0-2-0, p2-2-2, v2-3-2, r1-1-1.

Female: Unknown.

Other material examined. None.

Distribution. Known only from the type locality in central Namibia.

Cyrioctea hirsuta, new species
Figs. 3–4

Type. Female holotype from Ugab River, Namibia (Apr. 25, 1987), deposited in the State Museum, Windhoek (SMN 40494).

Etymology. The specific name refers to the thick patch of setae on tibiae and metatarsi III.

Diagnosis. Females of this species have two unique leg modifications: the third tibiae and metatarsi have their dorsal and prolateral surfaces coated with a thick patch of stiff setae, and the first metatarsi and tarsi are elongated, virtually fused together, ventrally excavated, lined ventrally with two lateral rows of short, stiff macrosetae (of which the retrolateral row is much longer and stronger), and have the
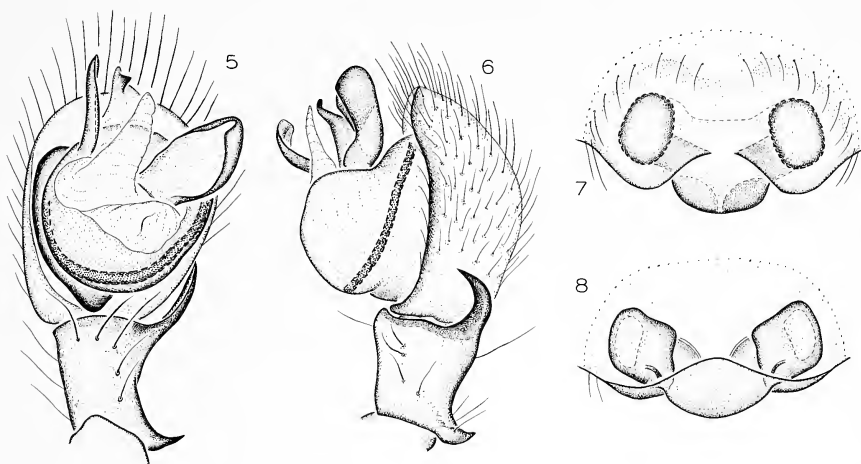
Figs. 5–8. 5. *Cyrioctea namibensis,* left male palp, ventral view. 6. Same, retrolateral view. 7. *C. raveni,* new species, epigynum, ventral view. 8. Same, dorsal view.

teeth of the paired claws clustered on a proximal ledge. Although it is conceivable that this species represents the female of *C. whartoni* or *C. namibensis,* the absence of any indication of either leg modification in the males of those species makes that possibility seem unlikely.

Male: Unknown.

Female: Total length 5.46. Carapace 2.72 long, 1.58 wide. Femur II 1.13 long. Eye sizes and interdistances: AME 0.05, ALE 0.09, PME 0.08, PLE 0.10; AME-AME 0.14, AME-ALE 0.01, PME-PME 0.12, PME-PLE 0.10, ALE-PLE 0.11; MOQ length 0.37, front width 0.25, back width 0.28. Epigynal scape broad (Fig. 3); spermathecae circular (Fig. 4). Leg spination: femora I-IV d0-0-0, p0-0-0, r0-0-0; patellae: II p0-0-1; III d0-0-1, r0-0-0; IV d0-0-0, p0-0-0, r0-0-0; tibiae: I p0-0-0, v0-0-0; II p1-0-1, v0-0-0; III d1-0-1, p2-1-0, v0-0-1p, r0-0-1; IV d1-0-0, p0-0-0, v1p-1p-1p, r1-0-1; metatarsi: I p0-0-0, v0-0-0, r0-0-0; II p0-0-1, v0-0-1p, r0-0-0; III d0-0-0, p1-1-1, v0-0-1p, r1-1-1; IV d0-0-0, p1-1-2, v0-0-2, r1-1-1.

Other material examined. None.

Distribution. Known only from the type locality in northern Namibia.

Cyrioctea namibensis, new species
Figs. 5–6

Types. Male holotype and paratype taken in pitfall traps in the Namib Desert gravel plains at the Arandis site of the Rossing Mine survey, latitude 22°22′S, longitude 14°59′E, Namibia (July 3–10, 1984; J. Irish, H. Rust), deposited in the State Museum, Windhoek (SMN 38160); male paratype (same data) deposited in the American Museum of Natural History.

Etymology. The specific name refers to the type locality.

Diagnosis. Males can be distinguished from those of all other known species by the presence of both proximal and distal retrolateral tibial apophyses (Fig. 6).

Male: Total length 2.93. Carapace 1.72 long, 1.01 wide. Femur II 1.13 long. Eye

A NEW *CRYPTOCELLUS* (ARACHNIDA: RICINULEI) FROM BRAZIL

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Abstract. —A new ricinuleid, *Cryptocellus adisi,* is described from Amazonas, Brazil; it resembles *C. albosquamatus* of Guyana and *C. narino* of Colombia in having the body and legs coated with navicular setae, but differs in genitalic characters.

Long regarded as among the rarest of invertebrates, ricinuleids are now known to be locally abundant in certain areas, but the majority of described species are still represented in collections by very few specimens (see Platnick and Paz, 1979:table 1, for a listing of the known adults from South America and their depositories). Hence it was with great interest that I recently examined an extensive collection of these animals amassed by Dr. Joachim Adis of the Max-Planck-Institut, and his collaborators, in the course of their long-term ecological studies of terrestrial invertebrates in the inundation forests of the regions around Manaus in Amazonian Brazil (see Adis, 1984). As expected, the majority of the 89 specimens (taken in a non-flooded area 50 m from a blackwater inundation forest site) are nymphs and therefore lack the genitalic characters necessary for specific identification, and the majority of the adults belong to *Cryptocellus becki* Platnick and Shadab (1977), originally described from the Reserva Ducke near Manaus. One female and five males of that species were extracted by the Kempson method from soil 0–7 cm deep in a secondary dryland forest at Rio Tarumã Mirím by J. M. Gomes Rodrigues between July and December of 1982 and 1983.

Of special interest, however, was the presence in the collection of three males and two females (as well as several nymphs) of a much smaller new species, described below, that resembles the Guyanan species *Cryptocellus albosquamatus* Cooke (1967) and the Colombian species *C. narino* Platnick and Paz (1979) in having the cephalothorax, abdomen, and legs coated with large, white, navicular setae. Scanning electron micrographs of these complex and peculiar structures can be found in Platnick and Shadab (1977:figs. 7, 8); they also occur in some African *Ricinoides* (Legg, 1976:pl. 1).

The format of the description follows that of Platnick and Paz (1979). I thank Dr. M. U. Shadab of the American Museum of Natural History for help with the illustrations.

Cryptocellus adisi, new species
Figs. 1–5

Types. Male holotype and female allotype extracted from soil 0–7 cm deep in a secondary dryland forest at Rio Tarumã Mirím, latitude 3°02′S, longitude 60°17′W,
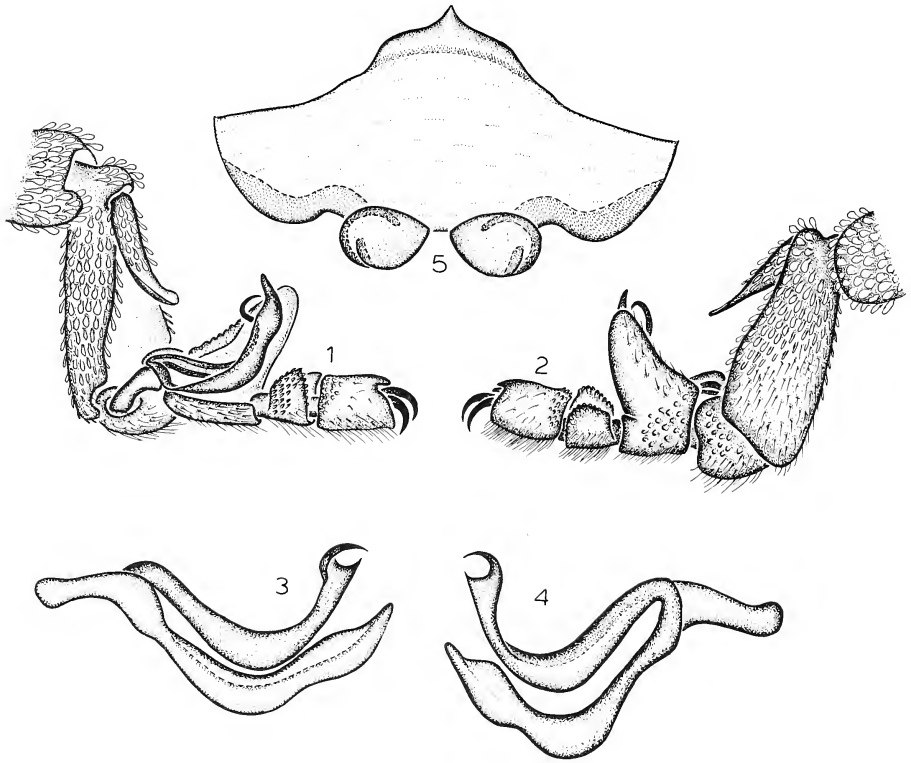
Figs. 1–5.   *Cryptocellus adisi.* 1. Male leg III, anterior view. 2. Male leg III, posterior view. 3. Male copulatory apparatus, anterior view. 4. Male copulatory apparatus, posterior view. 5. Female genital lip and spermathecae, posterior view.

Amazonas, Brazil (24 Aug. 1983; J. M. Gomes Rodrigues), deposited in Instituto Nacional de Pesquisas da Amazônia (INPA); single male and female paratypes (same data), deposited in American Museum of Natural History; male paratype (same data except collected 25 Aug. 1982), deposited in INPA.

Etymology. The specific name is a patronym in honor of Dr. Joachim Adis, in recognition of his numerous contributions to our knowledge of Amazonian arthropods.

Diagnosis. The structure of both the male and female genitalia (Figs. 1–5) distinguishes this species from the two other *Cryptocellus* species, mentioned above, that are similarly coated with white navicular setae; both the curved accessory piece of the male tarsal process (Figs. 3, 4) and the shape of the female spermathecae (Fig. 5) are diagnostic.

Female: Total length 3.16. Carapace 1.17 long, 1.24 wide near front of coxae III, where widest, reddish brown, darkest along lateral margins, with small, triangular translucent pale yellow areas at margins between coxae II and III; surface coated with white navicular setae, with small tubercles concentrated along midline and

posterior margin, without deep pits, deeply depressed behind translucent areas. Cucullus 0.49 long, 0.68 wide, reddish brown, proximal two-thirds coated with white navicular setae, distal one-third with long, white setae and numerous small tubercles; lateral lobes only slightly protuberant. Left chelicera: movable finger flattened posteriorly, not widened transversely, armed with five teeth increasing in length distally; fixed finger armed with five well separated teeth increasing in length distally. Sternal region with coxae I not meeting tritosternum; coxae II meeting along their posterior halves, their suture line only about half as long as that of coxae III; coxae IV meeting anteriorly. Abdomen 2.25 long, 1.95 wide near front of tergite 12, where widest, coloration and setation as in carapace except for dark orange articular membranes and ventral surface lacking white navicular setae along v-shaped anterior band reaching almost to rear of sternite 12 along midline; all surfaces with scattered tiny tubercles densest in transverse band on tergite 9, without pits; median plates of tergites 11–13 wider than long, with pair of submarginal depressions (occupying middle one-third of length on tergite 11, anterior one-half on tergite 12, anterior one-third on tergite 13), depressions lacking white navicular setae but with tubercles. Pygidium without notch in posterior dorsal or ventral margin of basal segment. Palpal coxae and trochanters red, distal segments orange; second trochanters and femora with white navicular setae; coxae, trochanters, and femora with numerous tiny tubercles; coxae apparently without thick white setae posteriorly; tibiae with long setae but with elevated tubercles restricted to distal tip of ventral surface. Leg formula 2341. Legs reddish orange, tarsi lightest, densely coated with white navicular setae except sparse on coxae and posterior trochanters, all segments with numerous tiny tubercles, without enlargements. Leg measurements:

	I	II	III	IV	Palp
Coxa	0.42	0.64	0.58	0.49	0.23
Trochanter I	0.26	0.39	0.30	0.38	0.24
Trochanter II	—	—	0.30	0.39	0.24
Femur	0.48	0.85	0.73	0.73	0.50
Patella	0.28	0.59	0.49	0.36	—
Tibia	0.45	0.68	0.55	0.53	0.75
Metatarsus	0.44	0.77	0.48	0.47	—
Tarsus	0.24	0.89	0.47	0.49	0.11
Total	2.57	4.81	3.90	3.84	2.07

Second legs slightly widened; femur I about 2.5, femur II about four times as long as wide. Tarsal claws thin, evenly curved. Posterior genital lip and spermathecae as in Figure 5.

Male: As in female, except for the following. Total length 3.15. Carapace 1.11 long, 1.28 wide. Cucullus 0.53 long, 0.75 wide, with fewer tubercles than in female. Left chelicera: movable finger armed with 8 teeth, most distal largest, almost fused to two next most distal, reduced teeth. Abdomen 2.03 long, 1.95 wide. Leg measurements:

	I	II	III	IV	Palp
Coxa	0.39	0.68	0.64	0.55	0.25
Trochanter I	0.30	0.41	0.44	0.38	0.26
Trochanter II	—	—	0.39	0.40	0.21
Femur	0.60	0.88	0.84	0.75	0.50
Patella	0.47	0.52	0.48	0.47	—
Tibia	0.54	0.78	0.62	0.57	0.85
Metatarsus	0.56	0.85	0.64	0.54	—
Tarsus	0.33	0.92	0.73	0.53	0.11
Total	3.19	5.04	4.78	4.19	2.18

Metatarsus and tarsus III as in Figures 1, 2; tarsal process as in Figures 3, 4.

Material examined. Only the types.

Distribution. Known only from the type locality, about 20 km upstream from Manaus, Brazil.

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COMMENT

REBUTTAL (=ERRATA):
GRADING THE MAKING OF A BOOK REVIEW

A recent review (Pakaluk, 1988) of Liebherr (1986) criticizes two aspects of that study. I hereby respond to the reviewer's contentions, as they are based on errors of interpretation, fact, and judgment.

The reviewer cites the subject of the major portion of the above monograph, the *Agonum extensicolle* group, as paraphyletic, and thus uninformative for phylogenetic and biogeographic analysis. He bases this statement on the cladistic analysis of the tribe Platynini based on 43 exemplar North American taxa that opens the study. The reviewer states, "This analysis is useful for understanding the placement of the *Agonum extensicolle* group and finding appropriate outgroup taxa (Pakaluk, 1988, p. 127)." This was not my rationale for conducting this analysis, as the entire chapter is devoted to conducting the first cladistic analysis of the Platynini, and comparing the results to earlier classifications (Jeannel, 1942; Lindroth, 1956; Habu, 1978). Species groups and genera are placed in the cladistic analysis, but I make no attempt to define monophyletic groups on a fine scale based on a study largely drawn from a regional fauna using exemplar taxa. As I stated, "The use of exemplars brings the associated risk that the ranges of character states are inadequately represented (Liebherr, 1988, p. 5)." Also, "The affinities among European and American species implies [*sic*] that a regional analysis will be unsatisfactory for determination of phylogenetic relationships within this group. Only a worldwide perspective will produce a stable classification (p. 26)."

The classification presented in Appendix 2 of the monograph is intended as a step toward defining groups with European and American species held in common. To this end, the genera recognized are based on type species of commonly misused platynine generic names. That the genera *Anchomenus, Platynus,* and *Agonum* each have basically different female reproductive tracts provides the means to place species of the world fauna as members of each of these lineages using derived states of the female tracts. As these names have been synonymized in nearly every possible combination over classificatory history (Habu, 1973), this advance is of some importance to carabid systematics. As a side note, the variation in the female reproductive tract within Platynini is substantial, and will become the major means of delimiting natural groups within the tribe. The species groups recognized within *Agonum* in Appendix 2 are modified from those of Lindroth (1966), with any changes from that classification based on the distribution of shared-derived character states.

In answer to the reviewer's contention that the *A. extensicolle* group is not defined monophyletically, the species group diagnosis is cited. The group is diagnosed using

4 derived character states; metallic coloration, mesocoxal setation, number of dorsal elytral setae, and antennal setation (Liebherr, 1986, pp. 25, 85). The first was not used in the tribal cladistic analysis as it is generally variable across the tribe, and appears to be positively correlated with life in fully insolated habitats. Thus diagnosed, the group is revised, and within-group phylogenetic relationships and biogeographic patterns are analyzed.

An indication of how I view the relationship of the tribal cladistic analysis to the within-*extensicolle* group cladistic analysis can be obtained by reading the rules of out-group analysis for the latter. To determine primitive states for the *A. extensicolle* group analysis, I used "Other species of *Agonum* and *Platynus,* as well as members of other tribes of Carabidae . . . (Liebherr, 1986, p. 144)." I did not specifically use *A. quadrimaculatum,* or any other single group within *Agonum* as the outgroup, as I have little confidence that the phyletic structure present in the exemplar analysis is stable for species-group relationships.

I believe the reviewer's dismay at my preliminary cladistic analysis lies in what can be called the pitfall of literal translation. Cladistic analyses of older more diverse groups are likely to lack some portion of the extant taxa, due either to the large number of taxa, or incomplete knowledge of the world fauna. If this fact is explicitly admitted, the cladogram scheme should not be considered grounds for making no-menclatural and classificatory changes beyond those judged reasonable by the reviser. We should not assume a cladogram to specify a classification unless specifically advised to do so. More importantly, we should not wait to do cladistic analysis until we believe all extant species in a monophyletic group can be included.

A second criticism I wish to respond to is the reviewer's rejection of Plio-Pleistocene speciation in the *A. extensicolle* group. He apparently bases his stance on Coope's (1979) statement, "modern work on fossil Coleoptera [has] found no evidence of morphological change during the latter part of the Quaternary, nor [is] there reason to believe that many species became extinct during this period (p. 249)." That species represented in northern latitudes in Quaternary time are extant today says nothing about the species not represented in the fossil record. Moreover, my citation of speciation timing in the *A. extensicolle* group involves diversification since the late Miocene to mid-Pliocene, the latest divergence event timed from 160,000–2,400,000 years ago. As another example of Pleistocene speciation in Carabidae, one can cite the Hawaiian platynine fauna of more than 111 species (Zimmerman, 1948), which occurs on islands ranging from less than one million years to 6.4 million years of age (Kaneshiro, 1983). Admittedly, much diversification could have occurred on older islands now submerged to the northwest of the present islands, but the 12 species endemic to Hawaii (Sharp, 1903) can be no older than the age of that island, at most one million years.

The reviewer also asks where platynine species listed in Matthews (1979) would fit in the cladistic analysis. The species listed are *Agonum bicolor, A. consimile,* and *Platynus cincticollis.* A rough idea of their placement can be obtained by inspection of the classification presented in Appendix 2 of Liebherr (1986) in light of the clado-gram of figure 10 (p. 22). The late-Miocene dating of species cited by Matthews (1979) is uninformative with regard to timing of divergence events within the *A. extensicolle* group. —*James K. Liebherr, Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York 14853-0999.*

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BOOK REVIEWS

Kin Recognition in Animals.—D. J. C. Fletcher and C. D. Michener, eds. 1987. John Wiley & Sons Ltd., New York. 465 pp. Hardbound $77.95.

Recognition of kin is a critically important ability in most animals; its functional significance impinges upon all social interactions among conspecific individuals, including mating. As biologists have become more interested in the evolution of social behaviors, the literature on kin recognition has increased dramatically. This book makes a large proportion of this literature accessible in a single volume by compiling information across taxa from isopods to humans, and it is more cohesive and comprehensive than some collected works. Four introductory chapters establish the context for eight review chapters, six of which cover the literature on kin recognition for a broadly specified taxonomic group. Of the two remaining chapters, one considers kin recognition in *Drosophila* and the other focuses on the desert isopod *Hemilepistus reaumuri.*

The volume contains several cohesive themes throughout, yet each chapter bears the stamp of the individual author(s). Following a short introductory chapter by D. J. C. Fletcher and C. D. Michener, E. O. Wilson provides a clear synopsis of the functions of kin recognition, provides a useful glossary of terms, and briefly touches on the bioassays, proximate mechanisms, genetics and economics involved. J. D. C. Fletcher briefly outlines the functions and mechanism of kin recognition and then focuses on methodological considerations. Proposed genetic mechanisms leading to the evolution of kin recognition systems are discussed succinctly by R. H. Crozier.

These chapters provide the framework for those that follow. E. B. Spiess summarizes the arguments for the rare male effect in *Drosophila* illustrating the potential importance of kin recognition in mate selection. A long and somewhat rambling chapter by K. E. Linsenmair is a fascinating account of research on the subsocial desert isopod *H. reaumuri* that includes a considerable amount of material not previously published. The chapter on primitively eusocial insects by C. D. Michener and B. H. Smith is fairly brief and concentrates primarily on the kin recognition systems of halictine bees and polistine wasps but also touches on bumble bees and vespine wasps. The review of kin recognition in highly social insects, by M. D. Breed and B. Bennett, covers the considerable information on honey bees and ants and points out the lack of information available for termites. These chapters on invertebrates are followed by a series of contributions on vertebrates.

For vertebrates other than primates, A. R. Blaustein, M. Beckoff, and T. J. Daniels provide an overview of empirical evidence followed by a consideration of mechanisms, functions and the direction of future research. Research on primates other than humans is reviewed by J. R. Walters, who calls for an increase in empirical studies aimed at illuminating recognition mechanisms in non-human primates. P. A. Wells' chapter discusses the largely inferential evidence of kin recognition in humans.

This impressive collection of scholarly review chapters is aptly concluded by W.

D. Hamilton, who discusses the application of evolutionary concepts such as kin recognition and nepotism to humans and the controversy such generalizations engender. He considers the possible role of nepotism in human history, and calls for preservation of and respect for human racial and cultural diversity.

The basic approach taken by this work is an evolutionary one. As such it is complementary to the excellent and somewhat broader volume on recognition by Colgan (1983), which takes a more mechanistic perspective. Though *Kin Recognition in Animals* is quite broad, certain taxa are not well covered, such as sessile, colonial invertebrates and fish.

This book, with its extensive reviews of kin recognition over a broad range of taxa, will be a valuable reference book for advanced students, teachers, and researchers in social behavior and is a must for anyone seriously interested in kin recognition.— *Penelope F. Kukuk, Department of Entomology, Cornell University, Ithaca, New York 14853.*

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Colgan, P. 1983. Comparative Social Recognition. John Wiley & Sons, Ltd., New York, 281 pp.

Pheromones of Social Bees.—John B. Free. 1987. Cornell University Press, Ithaca, New York. xiii + 218 pp. $29.95 (cloth).

In this modest 218 page compilation of research of the past 100 years, John Free applies his 30+ years of experience with bumblebees and honeybees to the task of summarizing our knowledge of the releasing and priming pheromones of the true honeybees, bumblebees, stingless bees, and even sweat bees, emphasizing, of course, *Apis mellifera.* Allomones and kairomones are by definition not addressed, nor are the semiochemicals of the non-eusocial bees, the latter having been summarized by Duffield et al. (1984). Pheromones, those ubiquitous intraspecific chemical messages that characterize Life, are the subject of this book, including queen, brood and worker pheromones.

The book is rightly organized by the sundry functional responses to pheromones, rather than by molecular class or glandular source. The functions are diverse, ranging from regulation of worker ovarian development and nestmate recognition to drone attraction and worker alarm. Free's task is not enviable, for the burgeoning literature of the biology of *Apis mellifera* is only exceeded by that of a few animals, such as the Norway rat and ourselves. Furthermore, social bees have been actively studied by groups on every continent, published in sometimes obscure or unexpected journals in several languages, and too often require careful *a posteriori* interpretation of an author's claimed evidences. Although Free may be a bit overly enthusiastic as to the sheer multiplicity of pheromones among the social bees, he is generally careful to weight conclusions judiciously as to whether they reflect independently confirmed pheromonal investigations, as yet unduplicated experimental results, or reports that

withstand alternative interpretations. This care is important, as much published research with *Apis mellifera* in particular necessarily involves rather artificial manipulations which can be prone to the introduction of artifacts, especially in the worker's behavioral responses.

In as much as sociality has arisen repeatedly among the bees, I am disappointed that Free did not develop more comparative evolutionary interpretations for the existence, functions, and glandular sources of pheromones of social bees. For instance, why is the Nasonov gland, releaser of the *Apis* worker's orientation pheromone, located near the dorsal tip of the worker's abdomen? Is an earlier purpose implied by homology, or are there analogous precedents from other social insects? Free brings little light to bear upon such evolutionary questions, but he does manage a carefully organized, descriptive summary of proximal function, complete with some innovative suggestions for apicultural applications. In surveying the literature, he also presents some of the methodologies of the chemical ecologist, though not those of the natural products chemist. The latter is clearly outside of his expertise.

The text has its share of accompanying figures, graphs, tables and flow charts, but for me, these are upstaged by his magnificently crisp and contrasty black-and-white photographs of bees-in-action. They verge on the artistic. Cited published references are pre-1985. His index is adequate. Free's message is clear: we know much about the pheromones of social bees, but far more lurks in the vast unknown. This book, in combination with Winston's (1987) and Seeley's (1985) books of the last several years, provide the callow melittologist, or at least apiculturist, with a coherent starting point from which to launch into those promising semiochemical unknowns without unwittingly reinventing the proverbial wheel. — *James H. Cane, Department of Entomology, Auburn University, Auburn, Alabama 36849.*

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ERRATA

Vol. 96, no. 2, pp. 140–175: The correct running head should be "STENOGASTRINAE."

Vol. 96, no. 2, p. 228: The correct caption for Figure 1 should be: "Wygodzinsky (center) in field, 1955, Brown Canyon, Baboqivari Mountains, Pima County, Arizona, with Floyd G. Werner (left) and George Daniel Butler, Jr.

INSTRUCTIONS TO AUTHORS

The *Journal of the New York Entomological Society* is devoted to the advancement and dissemination of knowledge of insects and related taxa. The costs of publishing the Journal are paid by subscriptions, membership dues, page charges, and the proceeds from an endowment established with bequests from the late C. P. Alexander and Patricia Vaurie. The Journal will consider for publication manuscripts of any length dealing with original research in entomology. Longer papers will be printed as articles, shorter ones as "scientific notes." Book reviews will be solicited by the Book Review Editor.

Manuscripts should be submitted in duplicate to: Dr. Randall T. Schuh, Editor, Journal of the New York Entomological Society, c/o Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024. All material must be double-spaced (including references, tables, captions, etc.) and prepared in the format of a recent issue of the Journal.

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JOURNAL OF THE NEW YORK ENTOMOLOGICAL SOCIETY

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A NEW SPECIES AND FIRST TRUE RECORD OF ISOMETOPINAE (HETEROPTERA: MIRIDAE) FROM MADAGASCAR

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Abstract. — A new species of Isometopinae, *Magnocellus madagascariensis,* is described from the spiny forest of southwestern Madagascar. This is the first actual record of Isometopinae from the island. Comparison is made between this species and other members of *Magnocellus.* Habitat notes, a habitus illustration, and a distribution map are provided.

The mirid subfamily Isometopinae is widely distributed, occurring on all continents except Antarctica and on many large islands as well. Madagascar is the last major tropical land mass to lack records of this group. Carvalho (1952) described *Biliola microscopica* as an isometopine based on a single female from Mt. d'Ambre, at the far northern end of the island, but Carayon (1958) subsequently transferred *Biliola* to the Anthocoridae, so that once again there were no actual records of isometopines from Madagascar. The present paper, however, reports a true isometopine from the spiny forest in the dry southwest, a new species in the predominantly African genus *Magnocellus.* This fills a significant zoogeographical gap in the distribution of the subfamily, and provides another link between the fauna of western Madagascar and that of southern Africa.

Magnocellus madagascariensis, new species

Diagnosis. M. madagascariensis may be immediately separated from the other known species of *Magnocellus* by the coloration of the pronotum, scutellum and hemelytra, which are entirely black except for a small dark yellow spot at the apex of the scutellum (Fig. 1).

Description. Brachypterous female. Small, ovate, total length 2.00 mm, maximum width 1.45 mm (Fig. 1); general coloration black, with dark yellow spot at apex of scutellum; head with vertex and upper frons dark yellow, eyes and ocelli dark red, central frons below eyes black with 4 broad transverse creamy white striae (Fig. 2), expanded lateral portions of lower frons below eyes black, posterior margin of head behind eyes and along base of vertex narrowly creamy white. Antennal segment I black; antennal segment II pale yellowish, gradually darkened to black on basal and distal ¼, extreme tip also narrowly pale; antennal segment III pale yellowish, gradually darkening on apical ⅓; antennal segment IV uniformly pale yellow; all antennal segments clothed with fine, recumbent, pale setae. Pronotum black, very narrowly smoky translucent along lateral margins; scutellum black, with small spot at extreme apex dark yellow; hemelytra black, membrane fumate; pronotum, scutellum and hemelytra evenly clothed with semi-recumbent pallid pubescence, membrane lacking pubescence. Ventral surface black; rostrum with alternating broad black and translucent brown sections, giving striped appearance; legs predominantly dark brown to
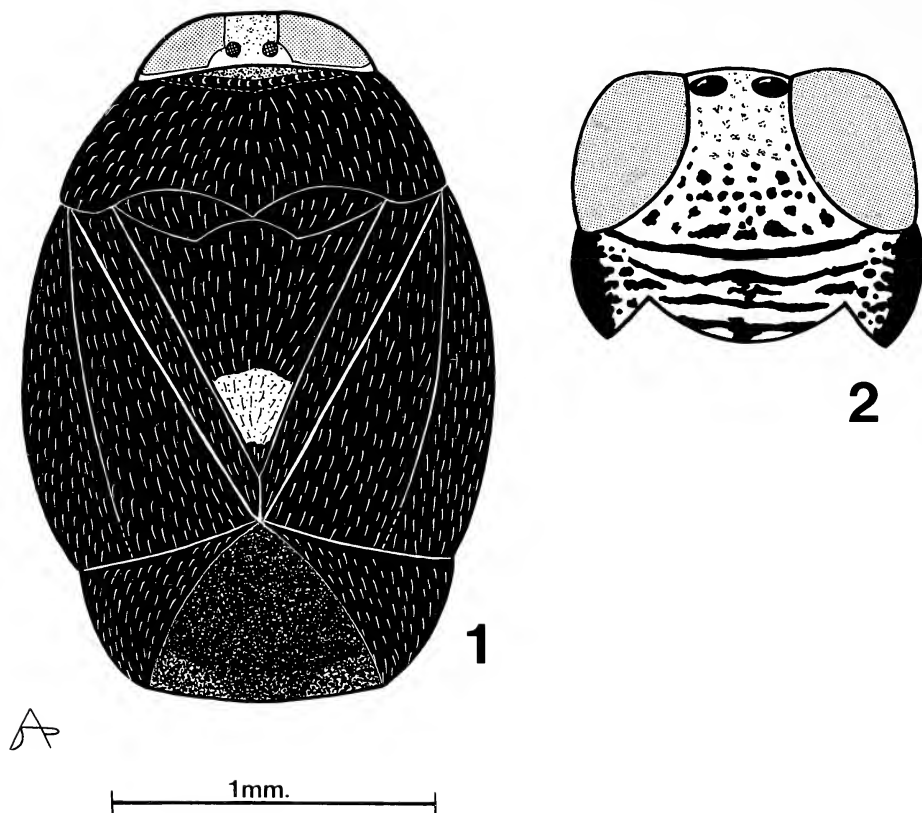
Figs. 1, 2. *Magnocellus madagascariensis.* 1. Female holotype, dorsal habitus, antennae and legs omitted. 2. Female holotype, frontal view of head.

black except for following pale yellowish: fore trochanters, tarsi, and distal half of fore tibia, middle coxae, trochanters, tibia and tarsi, hind coxae, trochanters, tarsi and extreme base of hind tibia.

Head vertical, lateral portions of lower frons expanded beneath eyes with small V-shaped notches on lower margins to accommodate antennae (Fig. 2); ocelli large, prominent, touching inner margins of eyes, interocellar distance slightly less than twice the width of an ocellus; length of head 0.51 mm, width across lower margins of eyes 0.68 mm, interocular space 0.18 mm, width of ocellus 0.05 mm, interocellar width 0.08 mm; length of rostrum 1.17 mm, reaching beyond hind coxae. Antennae with segment II more slender than segment I, lengths of segments I–IV: 0.08 mm; 0.44 mm; 0.31 mm; 0.18 mm. Pronotum convex, with very narrow collar along anterior margin marked by line of small punctations, lateral margins arcuate and explanate, posterior margin biconcave with sharp angle medially, length (midline) 0.36 mm, width 1.12 mm; scutellum convex, length 0.78 mm, basal width 0.82 mm; hemelytra with clavus strongly narrowing posteriorly, length of claval commissure 0.11 mm, distance from apex of clavus to apex of cuneus 0.72 mm.
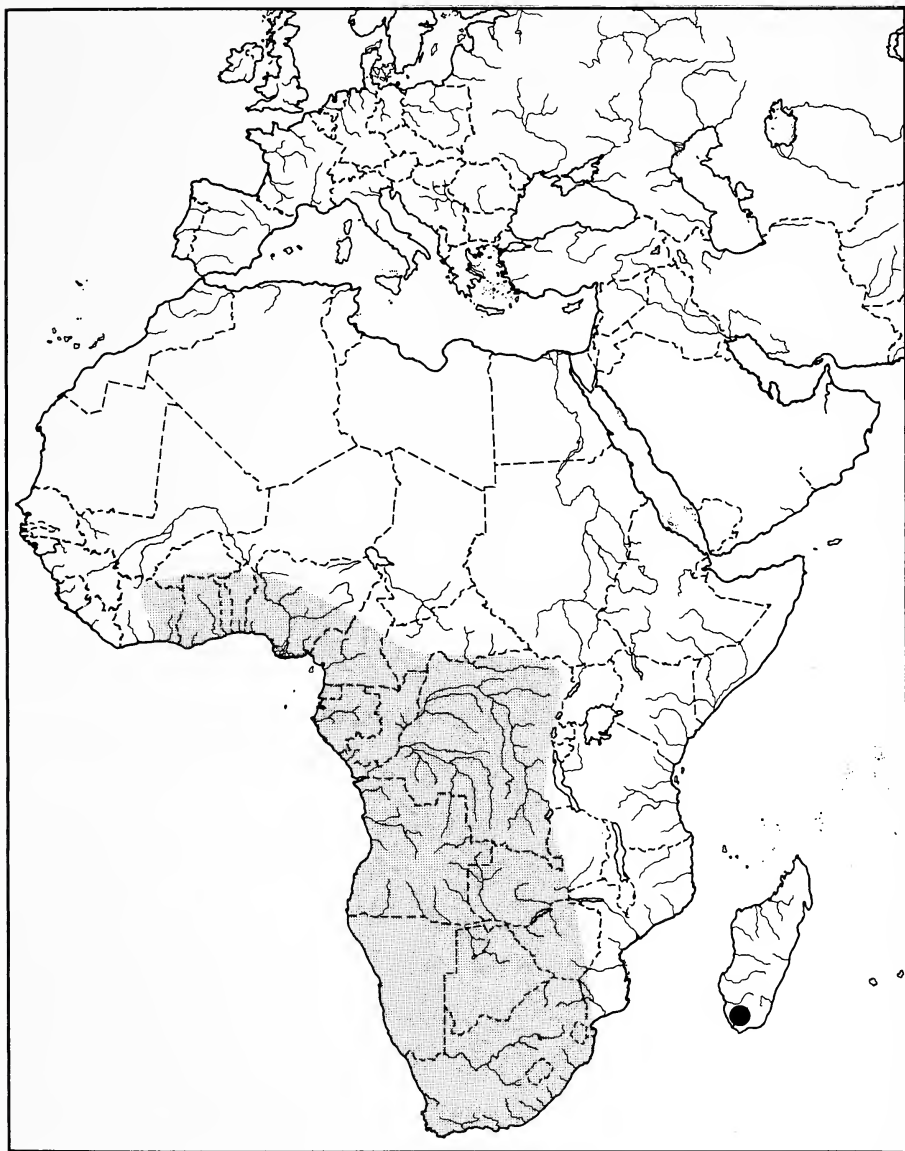
Fig. 3. Distribution of *Magnocellus* in Africa and Madagascar. Solid circle = *Magnocellus madagascariensis*; shaded area = range of remaining species in genus.

Discussion. In Slater and Schuh's (1969) key to the species of *Magnocellus, M. madagascariensis* n. sp. runs to *M. ghanaiensis* Smith, from which it may be separated by its dark fore and middle femora, and distinctive dorsal coloration. According to the above authors the dorsal coloration of *M. ghanaiensis* is predominantly light

brown, with a whitish band across the posterior margin of the pronotum, a mostly pale scutellum with limited dark markings basally and apically, and uniformly brown hemelytra. *M. madagascariensis* by contrast is almost entirely black, with contrasting dark yellow markings only on the vertex and the tip of the scutellum (Fig. 1). No other described species of *Magnocellus* shares this color pattern, most being either primarily brown or pale, or having white maculae on the hemelytra. In addition, *M. madagascariensis* also lacks fine pubescence on the membrane of the forewing, a character state shared with *M. ghanaiensis* Smith and *M. albifrons* Slater and Schuh.

The discovery of this species in Madagascar provides another link between the terrestrial heteropteran fauna of this island and that of southern Africa (Fig. 3). This is not surprising based on ecological considerations, since many of the dry deciduous forest and savannah formations of western Madagascar are quite similar in general appearance to corresponding habitats on the adjacent African continent.

Habitat data. The type specimen was taken while beating vegetation in a tract of spiny dry sclerophyllous forest growing on red sand soils just inland of the Mozambique Channel coast (for a more thorough review of this vegetative community see Rabesandratana, 1984). The dominant species here included baobabs (*Adansonia fony* Baillon), various succulent *Euphorbia* species, and octopus trees (*Didieria madagascariensis* Baillon). These formed a broken canopy, the understory of which was heavily overgrown with numerous types of dry deciduous shrubs. Most of these shrubs had leafed out and some were in bloom, due to the recent onset of the rainy season. The type specimen of *Magnocellus madagascariensis* was taken from one of the understory shrubs, but the capture was not noted until after departing the locality, thus a precise host association cannot be made. Although Isometopinae are thought to feed almost exclusively on scale insects (Ghauri and Ghauri, 1983), no scales were observed during our collecting.

Holotype. Female: MADAGASCAR, Tulear Prov., spiny forest 5 km N of Ifaty, 0–50 m, November 27, 1986, CL 2292, J. T. and D. A. Polhemus (USNM).

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REUTERIA CRAIGI: A NEW PLANT BUG FROM MISSOURI (HETEROPTERA: MIRIDAE: ORTHOTYLINAE: ORTHOTYLINI)

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Abstract. — *Reuteria craigi* is described as new from Missouri, where it occurs on sugar maple, *Acer saccharum* Marshall (Aceraceae). The male genitalia are illustrated. Henry's (1976) key is modified to incorporate the new species.

Members of *Reuteria* are characterized by black lines on each side of the 1st antennal segment which connect ventrally at the apex. They are small (3.7–4.7 mm), fragile, pale green, often with green blotches on the dorsum. *Reuteria* contains nine species; eight from eastern North America and one, *marqueti* Puton, from Europe.

Herein a new species of *Reuteria* is described and Henry's (1976) key is modified to incorporate it.

The following abbreviations are for institutions and collections cited in this paper: EMUM, Wilbur R. Enns Entomology Museum, University of Missouri, Columbia; NCSU, North Carolina State University, Raleigh, N.C; RLB, Robert L. Blinn Collection; USNM, U.S. National Museum of Natural History, Washington, D.C. All measurements are in millimeters.

Reuteria craigi, new species
Fig. 1

Diagnosis. Recognized immediately from congeners by the unique structure of the left paramere of the male. The left arm of the paramere is bifurcate and curved dorsad, as in *irrorata,* and the right arm is strongly curved apically, as in *wheeleri.*

Description. Holotype male: Length 4.00 (ranges of 9 paratypes and holotype, 3.95–4.30), width 1.33 (1.30–1.55). Dorsum: pale to white, marked with green; clothed with recumbent white or silvery pubescence. Head: width 0.63 (0.58–0.64), vertex 0.31 (0.31–0.33), tinged with green on clypeus and lorum. Rostrum: length 1.18 (1.13–1.25), reaching to middle of posterior coxae. Antennae: I, 0.38 (0.36–0.40), white, black lines stout; II, 1.25 (1.20–1.35), testaceous with narrow black annulus at base; III, 0.98 (0.96–1.00), testaceous; IV, 0.68 (0.54–0.68), testaceous. Pronotum: length 0.48 (0.45–0.50), width at base 0.94 (0.89–1.00), white, area of calli tinged with green. Hemelytra: translucent white, marked with green blotches on clavus and corium; scutellum and mesoscutellum white; outer margin of cuneus and apex of embolium tinged with green. Membrane: transparent, veins green. Venter: white.

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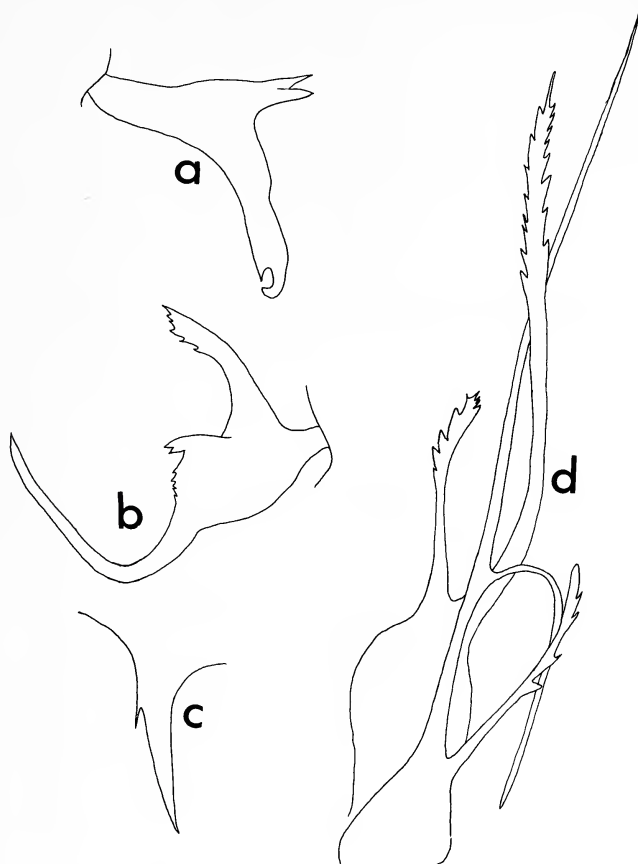
Fig. 1.   a–d. Male genitalia of *Reuteria craigi*. a. Left paramere. b. Right paramere. c. Tergal process. d. Spiculae of vesica.

Legs: pale, femora tinged with green, base of hind tibiae with black spot. Genitalia: Figure 1.

Female: length 3.85 (range of 6 paratypes, 3.85–4.15), width 1.47 (1.47–1.58). Head: width 0.60 (0.60–0.64), vertex 0.36 (0.33–0.36). Rostrum: 1.18 (1.18–1.27). Antennae: I, 0.40 (0.36–0.44); II, 1.24 (1.24–1.38); III, 1.04 (0.98–1.15); IV, 0.64 (0.60–0.67). Pronotum: length 0.47 (0.45–0.51), width at base 0.93 (0.93–1.04). Similar to male in color, markings and pubescence.

Holotype. Male: Missouri, Boone Co., Ashland Wildlife Area, 12-VI-1986, R. L. Blinn coll., taken on *Acer saccharum* (USNM).

Paratypes. 6 males, 5 females, same data as for holotype (EMUM, NCSU, RLB, USNM); 1 male, 1 female, same data as for holotype, 18-VI-1986 (EMUM); 1 male, Missouri, Boone Co., Columbia, 20-VI-1986, R. L. Blinn coll., taken at blacklight (EMUM); 1 male, Missouri, Boone Co., Columbia, 25-VI-1986, R. L. Blinn coll., taken on *Acer saccharum* (EMUM).

Etymology. This species is named in honor of Dr. Wilfred S. Craig, Department of Entomology, University of Missouri, Columbia, who has done much to increase our knowledge of the insects of Missouri and foster my interest in entomology.

Discussion. Henry's (1976) key is modified to include *craigi* as follows:

6. Left arm of right clasper long, slender, curved upward; tergal process slender with lateral branch spine-like 6a
–   Left arm of right clasper short and stout; tergal process short, stout, without spine-like lateral projection .... *irrorata* (Say)
6a. Left arm of left clasper unbranched, curved ventrad .... *wheeleri* Henry
–   Left arm of left clasper bifurcate, straight .... *craigi,* n. sp.

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BIOLOGY AND SEASONAL HISTORY OF
RHOPALUS (BRACHYCARENUS) TIGRINUS, WITH
DESCRIPTIONS OF IMMATURE STAGES
(HETEROPTERA: RHOPALIDAE)

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Abstract.—Seasonal history and habits are presented for *Rhopalus* (*Brachycarenus*) *tigrinus* Schilling, based mainly on observations made in Pennsylvania during 1980–1984. Nymphs and adults of this multivoltine Palearctic rhopalid recently recorded in eastern North America feed on reproductive structures of crucifers. Developmental times of the immature stages and data on premating period, fecundity, and longevity are given. The egg and nymphal stages are described, and scanning electron photomicrographs are provided for the egg and instars I–II and V.

Rhopalus (*Brachycarenus*) *tigrinus* Schilling, a scentless plant bug (Rhopalidae), is the widest ranging species of the genus (Göllner-Scheiding, 1983). Its natural range includes much of the Palearctic region, including Afghanistan and Pakistan but not the British Isles or Japan (Göllner-Scheiding, 1978; Ahmad, 1980). First detected in North America in Cumberland Co., New Jersey (Hoebeke, 1977), this immigrant species is now known from an additional county in New Jersey (Camden); Long Island, New York; Philadelphia and near Harrisburg, Pennsylvania (Hoebeke and Wheeler, 1982); and Baltimore, Maryland (Wheeler, 1984). Recent collections by AGW in 1987 also place it in Kent Co., Maryland (near Massey) and in Atlantic Co., New Jersey (Hammonton). Hoebeke and Wheeler (1982) provided a diagnosis, key, and illustrations allowing *R. tigrinus* to be distinguished from adults of the 15 other rhopalid species known to occur in eastern North America and recorded several crucifers (Cruciferae = Brassicaceae) as host plants. Here, we give notes on seasonal history, report on laboratory rearing, and describe and illustrate the immature stages.

MATERIALS AND METHODS

Field observations were made irregularly during 1980–1981 and 1984 on a population of *R. tigrinus* at the Enola railroad yards near Harrisburg, Pennsylvania. The sketch of seasonal history presented also is based on observations and collections made during 1979–1984 at Philadelphia; Baltimore; Medford and Yaphank, Long Island, New York; and Camden and Vineland, New Jersey.

Data on duration of immature stages, premating and preoviposition times, fecundity, and longevity are based on laboratory rearing of *R. tigrinus* at Ithaca, New York, and Harrisburg, Pennsylvania; both colonies originated from adults (4 male, 8 female) collected at Vineland, New Jersey, during 26–28 May 1979.

At Ithaca, two pairs were placed in individual large plastic boxes (26.5 cm × 19

Table 1.   Duration (in days) of immature stages of *Rhopalus tigrinus* reared in laboratory at Ithaca, New York (22–26°C) and Harrisburg, Pennsylvania (20–22°C); Harrisburg data are given in parentheses.

Stage	No. of observations	Range	Mean ± SD	Cumulative mean age
Egg	142 (14)	5–18 (8–9)	9.02 ± 0.02 (8.64 ± 0.04)	9.02 (8.64)
Nymphal stages				
I	47 (12)	2–9 (3–6)	3.91 ± 0.04 (4.42 ± 0.08)	12.93 (13.06)
II	38 (11)	1–5 (2–5)	2.37 ± 0.02 (2.82 ± 0.09)	15.30 (15.88)
III	34 (8)	1–3 (2–6)	2.06 ± 0.02 (3.38 ± 0.15)	17.36 (19.26)
IV	28 (4)	2–5 (3–6)	3.39 ± 0.03 (3.75 ± 0.38)	20.75 (23.01)
V	15 (—[a])	3–8 (—)	4.67 ± 0.08 (—)	25.42 (—)

[a] —, No observations.

cm × 10 cm), and single females were set up in two smaller plastic containers (8 cm diam., 2 cm deep). Both types of rearing containers were provided a water source and a sprig of shepherd's-purse, *Capsella bursa-pastoris* L. (Cruciferae), bearing flowers and fruits. They were maintained at room temperature (22–26°C) under natural photoperiod (window light). Host material was renewed every 2–3 days. Eggs deposited in rearing containers were assigned numbers, observed for hatching, and the resulting nymphs checked daily for ecdysis. Observations continued until three generations were completed (mid-September). The last generation was reared on peppergrass, *Lepidium virginicum* L. (Cruciferae).

At Harrisburg, two pairs and two females were set up in a manner similar to that used at Ithaca except that cultures were kept at 20–22°C and a 12-hr photoperiod. The first through fourth stadia are based on few observations owing to difficulties in rearing this rhopalid. Because all fifth instars died before molting, the fifth stadium was not determined.

BIOLOGY

Laboratory observations. From eggs laid approximately the same time, males emerged slightly before females (usually only 1 day or less). After a premating period of 3–5 days (N = 2), pairing occurred quickly without apparent courtship ritual. Pairs assumed an end-to-end position that is typical for rhopalids (e.g., Woodward, 1952; Wheeler, 1977; Paskewitz and McPherson, 1983) and usually remained *in copula* for several hours. Multiple matings (3–7 times) were common for the three pairs observed. After a 2-day preoviposition period (N = 2), eggs were deposited singly or in small clusters on host fruits, or on surfaces of the rearing containers. The fecundity of 2 virgin females averaged 101 (range 73–132); that of 4 field-collected, probably nonvirgin females averaged 86 (range 49–159). Eggs, which are pale yellow-orange when deposited, begin to darken within 2–3 days; by the fifth or sixth day they are dark brown to black, and the reddish eyes and abdominal segmentation can be seen through the chorion. By day 7 the sides become noticeably sunken, eye pigmentation is well defined, and the bristlelike setae of the nymphs are readily visible. Table 1 shows an average incubation period of about 9 days, although 6–8 days was typical
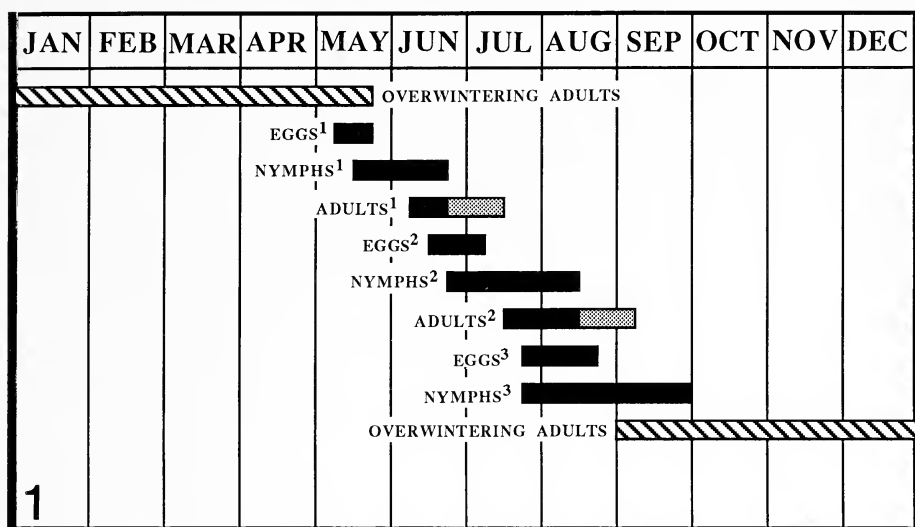
Fig. 1. Proposed seasonal occurrence of *Rhopalus* (*Brachycarenus*) *tigrinus* in eastern North America based on field and laboratory observations. [Superscript numbers refer to generations (i.e., 1 = 1st generation, etc.); stippled areas after "ADULTS 1 and 2" refer to periods of probable adult longevity, but specimens not actually observed.]

of the first two generations reared at room temperature and 10–12 days for the third generation.

Nymphs fed on reproductive structures of the crucifers, especially the fruits (siliques). The second and third stadia were the shortest, with total development time averaging 25.4 days (Table 1). Just as the incubation period was greater for the third compared to the first or second generation, the developmental period for first-stage nymphs was considerably longer in the third generation (5–9 days vs. 2–4 days).

Adults also fed on the crucifer fruits. The longevity of 2 first generation males observed was 10 and 13 days; that of 2 females, 14 and 26 days.

Field studies. Although *Rhopalus tigrinus* was sampled only at irregular intervals, our observations on development of field populations corresponded well with data obtained from the rearing of three generations in the laboratory. The phenological sketch (Fig. 1) that follows is based on field data, with the number of generations extrapolated from laboratory observations.

In the Palearctic region, adults of *R. tigrinus* are known to overwinter (Dupuis, 1953). Kiritchenko (1951) recorded nearly 100 adults hibernating in nests of several bird species. In Pennsylvania we swept an adult from crucifers as early as the first week of May and collected several overwintered adults, including mating pairs, during late May. Adults collected on 4 June at Philadelphia probably also were overwintered individuals. Teneral adults and instars II–V of a first generation were present in New Jersey during mid-June. *Capsella bursa-pastoris* was the most common early-season host; adults only were taken on other crucifers: *Arabidopsis thaliana* (L.), *Sisymbrium altissimum* L., and *Thlaspi perfoliatum* L. Adults and nymphs of a second generation

were observed at Baltimore during mid-July and early August; eggs and instars I–V of this generation were found at Philadelphia in mid- and late July. Adults and nymphs of all stages collected at Philadelphia in early September are believed to represent a third brood; these adults were not observed to mate or oviposit in the laboratory. Three adults and one third instar taken at Harrisburg on 20 September probably also belonged to this generation. Second and third generations developed on *Lepidium virginicum,* the only native plant among the known North American hosts of *R. tigrinus.*

In North America this rhopalid appears to be a crucifer specialist and the only member of the family known to feed on plants of the mustard family (see Schaefer and Chopra, 1982 and Schaefer and Mitchell, 1983 for food plants of world Rhopalidae). Stichel (1960) reported that *R. tigrinus* feeds on several crucifers in Europe, Popov (1965) listed it from *Artemisia* (Compositae) and Labiatae, Kerzhner (1967) characterized it as a "general feeder" that seems to prefer Cruciferae, and Lipa et al. (1977) reported its collection from numerous crucifers in central Europe. A preference for legumes (Gulde, 1921) and chenopods (Wagner, 1966) has been noted in the European literature, but occurrences on noncruciferous plants may be "sitting records" rather than actual hosts. We doubt whether *R. tigrinus* is a general feeder in the Old World, but the possibility of its developing on plants other than crucifers should not be eliminated. As Fox and Morrow (1981) stressed, specialization may be a local phenomenon of a population, with the species showing a wider host spectrum throughout its geographic range.

DESCRIPTION OF IMMATURE STAGES

Descriptions of the egg and nymphal instars are modified after the format and phrasing presented in Yonke and Medler (1969), Yonke and Walker (1970), Paskewitz and McPherson (1983), and Wheeler and Miller (1983). Puchkov and Puchkova (1956) provided illustrations of the egg and third-instar nymph of *R. tigrinus,* and also measurements of the nymphal stages. Herein, we provide scanning electron micrographs of the egg, and first-, second-, and fifth-instar nymphs of *R. tigrinus.*

EGG (in alcohol, N = 10) (Figs. 2–4). Elongate-oval, with slight indentation on either side of median longitudinal ridge (Figs. 2, 3). Pale yellow-orange shortly after deposition, darkening significantly during incubation. Two raised, turret-shaped, aero-micropylar processes present, one situated near ventral rim of pseudoperculum and one below it (Figs. 3, 4). Chorionic surface, including pseudopercular cap, rugose, covered with numerous raised, circular projections (Fig. 2).

Length: 1.10 mm (range 1.10–1.15). Width: 0.38 mm (range 0.35–0.40).

Egg attached to host plant surface by adhesive along middle of ventral side, lacking short ventral attachment stalk characteristic of most rhopalid species (Southwood, 1956; Cobben, 1968).

Gross structure of the egg of *Rhopalus* (*Brachycarenus*) *tigrinus* is similar to that described for other Rhopalidae by Stokes (1950), Southwood (1956), Yonke and Walker (1970) and Wheeler and Miller (1983).

FIFTH INSTAR (in alcohol, N = 10) (Fig. 7). Dorsum of head, thorax, and abdomen moderately densely setose, with long, bristlelike setae arising from minute papillae and chalazae. Chalazae of mesotergum and abdominal terga multisetiferous,
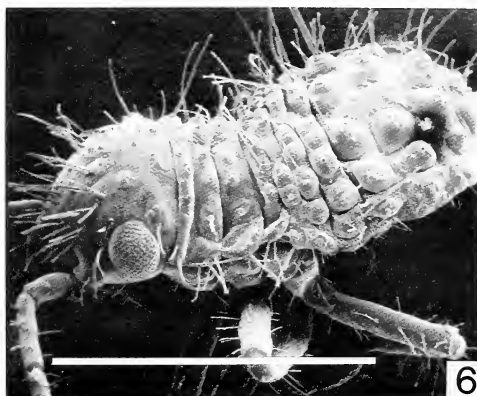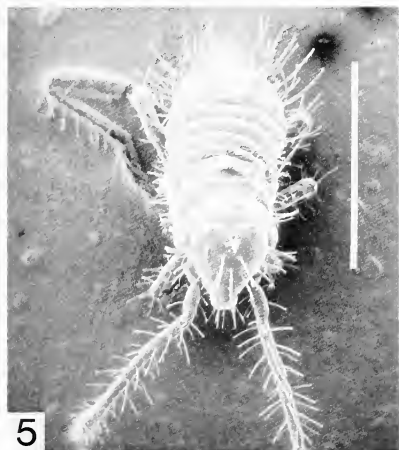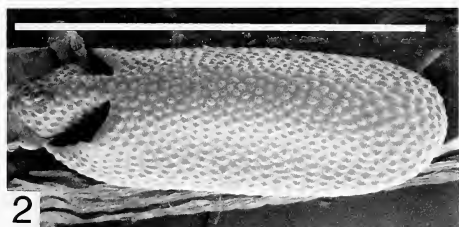
Figs. 2–6.   Egg and nymphal stages of *Rhopalus* (*Brachycarenus*) *tigrinus*.   2. Hatched egg, dorsolateral aspect. 3–4. Schematic representation of dorsal (3) and lateral (4) aspects of the egg showing position of 2 aero-micropylar processes, pseudopercular cap, and broad mid-longitudinal ridge of dorsum. 5. First instar, frontal dorsal aspect. 6. Second instar, dorsolateral aspect. All scale bars = 1 mm.

arranged in transverse rows. Body relatively pyriform, slightly dorsoventrally flattened.

Color variable among live specimens but generally brown-green with various dark infuscations, and dark spotting at base of setae on antennae and legs; color fading to pale white or yellow in alcohol-preserved specimens. Apices of antennal segments II and III, entire segment IV, some dorsal aspects of head, calli, and portions of posterior margin of pronotum, mesonotum, metanotal wing pads, and apices of mesonotal wing pads infuscated. Dark spots of legs sometimes coalescing to form bands, especially on femora. Eyes reddish. Dorsal and ventral surfaces of head, thorax, and abdomen spotted with red; collectively, in form of transverse striping on abdominal terga. Chalazae of abdominal terga heavily sclerotized, dark brown to black. Dorsal and ventral surfaces of body and appendages moderately densely covered with mixture of black and pale setae; setae of prominent abdominal chalazae black, those of general body surfaces white with some darker banding.

Length: 4.57 mm (range 4.10–6.40). Pronotal length: 0.61 mm (range 0.55–0.68).
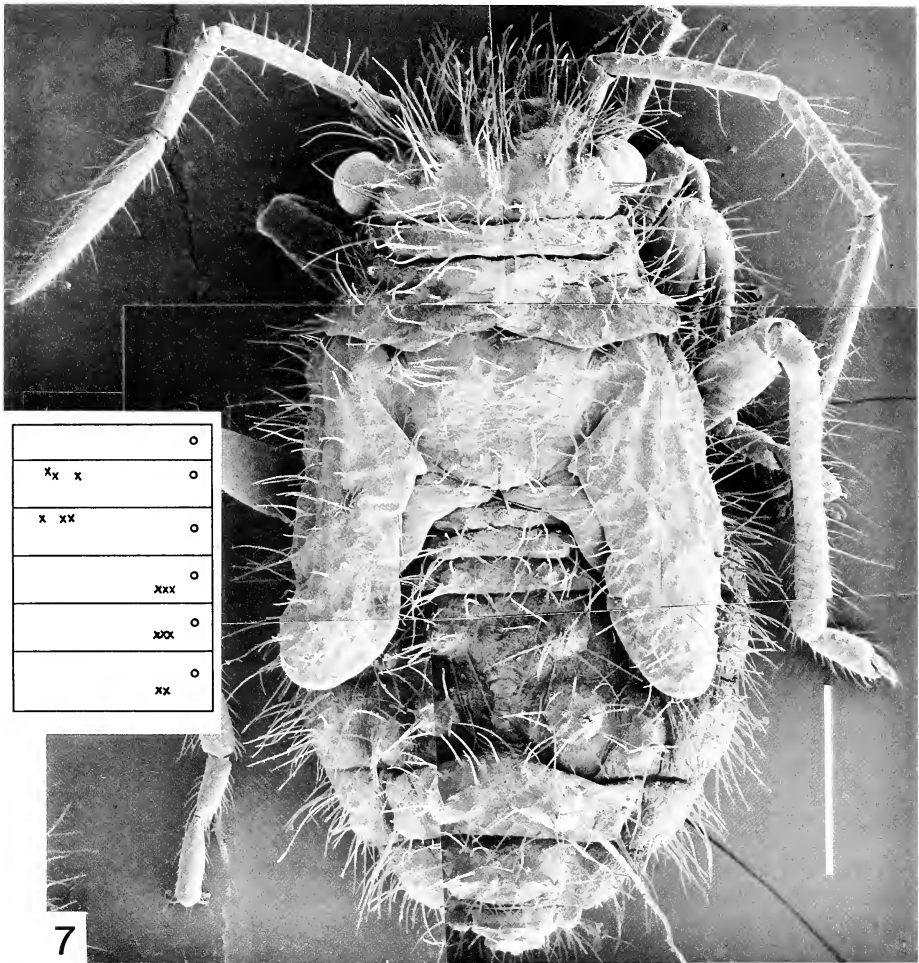
Fig. 7.   Fifth instar of *Rhopalus* (*Brachycarenus*) *tigrinus,* dorsal aspect, and (insert) tricho-bothrial pattern of abdominal sterna II–VII (x = position of trichobothria, and o = position of spiracles). Scale bar = 1 mm.

Basal pronotal width: 1.50 mm (range 1.30–1.65). Outer ocular width: 1.38 mm (range 1.30–1.50). Interocular width: 0.88 mm (range 0.83–0.98). Antennal lengths, I: 0.46 mm (range 0.43–0.50); II: 0.75 mm (range 0.70–0.80); III: 0.63 mm (range 0.60–0.68); IV: 0.98 mm (range 0.95–1.05).

Head. Antennal segments cylindrical; segment I short, broad; segments II–IV elongate, covered with long, erect (black and pale) setae, II slightly longer than III; segment IV apically pointed, with apical ½, between long setae, densely covered with minute setulae. Jugum extending to at least ⅔ length of tylus; both densely covered with long, bristlelike, black setae; antenniferous tubercle lacking. Labium extending to

middle of mesocoxae. Eyes large, prominent; dorsal surface of frons and occiput densely covered with long, black, bristlelike setae.

Thorax. Pronotum roughly trapezoidal, transverse, surface moderately densely covered with long, bristlelike setae; calli present, crescent-shaped; meso- and metathoracic wing pads extending to abdominal segment IV or V. Mesonotum with 2 prominent chalazae on either side of median line. Legs moderately densely covered with long, erect setae. Protibia with 3 black, strong setae in row on outer surface. Mesotibia with 1 black, strong seta at basal ⅓ of outer surface. Metatibia with 1 black, strong seta at middle of outer surface. Tarsi 2-segmented; pretarsi with 2 claws and 2 prominent pulvilli.

Abdomen. Four prominent chalazae on disc of terga III–VII, each bearing numerous long, bristlelike, black setae. Subdorsal pair of chalazae of terga I–V broadly separated along midline; width between chalazae gradually increasing in each succeeding segment, width broadest on tergum V. Pair of subdorsal chalazae of tergum VII nearly confluent along midline. Ventral segments moderately densely setose, with short, erect, pale setae. Pattern of trichobothria on ventral segments II–VII as in Fig. 7 (see insert).

Tergum I with median papilla and single transverse row of setae on either side, setae nearest midline on slightly raised tubercle. Two dorsal abdominal scent gland openings present, one between terga IV–V and one between terga V–VI; tergum V constricted at midline. Dorsum of terga VIII and IX with dark sclerotized plate.

FOURTH INSTAR (in alcohol, N = 5). Form and coloration as in fifth instar; chalazae of abdominal terga IV–VII and dorsal plates of terga VIII and IX strongly infuscated. Reddish spots of abdomen coalescing, forming transverse stripes. Wing pads reaching abdominal segment III.

Length: 3.53 mm (range 2.88–4.25). Pronotal length: 0.37 mm (range 0.29–0.54). Basal pronotal width: 1.10 mm (range 1.08–1.15). Outer ocular width: 1.05 mm (range 1.00–1.10). Interocular width: 0.67 mm (range 0.65–0.72). Antennal length, I: 0.36 mm (range 0.36); II: 0.52 mm (range 0.50–0.54); III: 0.47 mm (range 0.45–0.50); IV: 0.71 mm (range 0.65–0.76).

THIRD INSTAR (in alcohol, N = 5). Coloration similar to fourth instar; wing pads weakly developed, appearing as small lateral lobes.

Length: 2.57 mm (range 2.34–2.88). Pronotal length: 0.20 mm (range 0.18–0.25). Basal pronotal width: 0.84 mm (range 0.79–0.90). Outer ocular width: 0.86 mm (range 0.79–0.88). Interocular width: 0.55 mm (range 0.54–0.58). Antennal length, I: 0.25 mm (range 0.23–0.27); II: 0.45 mm (range 0.43–0.47); III: 0.37 mm (range 0.36–0.39); IV: 0.55 mm (range 0.54–0.57).

SECOND INSTAR (in alcohol, N = 2) (Fig. 6). Body pyriform; nearly pale, eyes sometimes reddish. Black, bristlelike setae of head, thorax and of chalazae of abdominal terga IV–VII prominent. No wing pad development.

Length: 1.57 mm (range 1.46–1.68). Pronotal length: 0.12 mm (range 0.11–0.13). Basal pronotal width: 0.56 mm (range 0.53–0.58). Outer ocular width: 0.53 mm (range 0.47–0.59). Interocular width: 0.36 mm (range 0.31–0.40). Antennal length, I: 0.14 mm (range 0.12–0.16); II: 0.28 mm (range 0.24–0.33); III: 0.28 mm (range 0.25–0.32); IV: 0.39 mm (range (0.35–0.44).

FIRST INSTAR (in alcohol, N = 10) (Fig. 5). Body elongate-pyriform; less dorsoventrally flattened than later instars. Coloration similar to second instar.

Length: 1.31 mm (range 0.95–1.57). Pronotal length: 0.14 mm (range 0.11–0.18). Basal pronotal width: 0.39 mm (range 0.36–0.42). Outer ocular width: 0.43 mm (range 0.41–0.45). Interocular width: 0.30 mm (range 0.29–0.33). Antennal length, I: 0.14 mm (range 0.13–0.15); II: 0.26 mm (range 0.24–0.29); III: 0.25 mm (range 0.24–0.27); IV: 0.37 mm (range 0.35–0.39).

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A REVISION OF THE GENUS *SYMPHEROBIUS* BANKS (NEUROPTERA: HEMEROBIIDAE) OF AMERICA NORTH OF MEXICO WITH A SYNONYMICAL LIST OF THE WORLD SPECIES

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Abstract. —The species of the genus *Sympherobius* of America North of Mexico are revised. Two species groups containing seventeen species are recognized. Two species, *S. constrictus,* from California, and *S. quadricuspis,* from Arizona, are described as new. The previously unknown male of *S. pictus* is also described. Four new specific synonyms are proposed (junior synonym(s) first): *S. brunneus* Nakahara and *S. stangei* Nakahara = *S. angustus* (Banks), *S. gracilis* Carpenter = *S. umbratus* (Banks) and *S. texanus* Nakahara = *S. killingtoni* Carpenter. A lectotype is designated for *S. perparvus* (McLachlan). Annotated synonymical listings summarize the existing literature on each species. Species ranges are summarized and mapped, including known records from regions extralimital to the continental United States and Canada. The relative relationships among the treated species are inferred from a cladistic analysis. An integrated key using forewing and male genitalic characters is presented. The following new terms are proposed for male genital structures or their subdivisions: gonopons, hemigonarcus, extragonarcus, intragonarcus, intrahemigonarcus, extrahemigonarcus, gonopleuron, gonoplax, paragonarcal membrane, pseudomediuncus, basipseudomediuncus and distopseudomediuncus. The monobasic Neotropical genus *Sympheromima* Kimmins is proposed as a new synonym of *Sympherobius.* A synonymical listing of the world species of *Sympherobius* is appended. In this list two new combinations, *Sympherobius marginata* (Kimmins) [from *Sympheromima*] and *Sympherobius exiguus* (Navás) [from *Micromus*] are proposed.

The hemerobiid genus *Sympherobius* Banks contains 54 currently recognized species distributed throughout the Nearctic (17 species), Neotropical (17), Palearctic (19) and Ethiopian (1) faunal regions. A comprehensive synonymical listing of these species is given in Appendix 1. Although *Sympherobius* has never been revised on a worldwide basis, relatively recent taxonomic treatments of the genus are available for the following regions: Amazon Basin (Penny and Monserrat, [1985] 1983), Cuba (Alayo, 1968), Europe (Aspöck et al., 1980), U.S.S.R. (Makarkin, 1986), Japan (Kuwayama, 1962) and southern Africa (Tjeder, 1961).

In this paper the *Sympherobius* species found in America north of Mexico are revised. Seventeen species are recognized from this region. Distributional and biological data are summarized for each species and an identification key is provided. The phylogenetic relationships among the seventeen species are inferred from a cladistic analysis. The clades indicated by this analysis serve as the basis for a preliminary classification of the Nearctic species.

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TAXONOMIC HISTORY OF NEARCTIC *SYMPHEROBIUS*

Shortly after establishing the genus in 1904, Banks (1905b) included seven North American species in *Sympherobius* and provided the first description of the genus. Fifteen species have subsequently been described from the Nearctic region by Banks (1911), Navás (1912, 1914a), Carpenter (1940), Gurney (1948) and Nakahara (1960, 1965a). The Nearctic species of *Sympherobius* were last revised by Carpenter (1940) who recognized 15 valid species from the region.

MATERIALS, METHODS AND GEOGRAPHICAL COVERAGE

Materials. More than 2,100 specimens of Nearctic *Sympherobius* from the 37 institutional collections listed below have been examined for this revision:

AMNH—American Museum of Natural History, New York; **ASUT**—Arizona State University, Tempe; **BMNH**—British Museum (Natural History), London; **CAS**—California Academy of Sciences, San Francisco; **CMP**—Carnegie Museum, Pittsburgh; **CSU**—Colorado State University, Fort Collins; **CU**—Cornell University, Ithaca; **FEM**—Frost Entomological Museum (Pennsylvania State University), University Park; **INHS**—Illinois Natural History Survey, Champaign; **ISU**—Iowa State University, Ames; **LACM**—Los Angeles County Museum, Los Angeles; **LSU**—Louisiana State University, Baton Rouge; **MCZ**—Museum of Comparative Zoology (Harvard University), Cambridge; **MSU**—Mississippi State University, Mississippi State; **NCSR**—North Carolina State University, Raleigh; **OKS**—Oklahoma State University, Stillwater; **OSU**—Ohio State University, Columbus; **OSUC**—Oregon State University, Corvallis; **PMY**—Peabody Museum (Yale University), New Haven; **SMEK**—Snow Museum of Entomology (University of Kansas), Lawrence; **TAMU**—Texas A & M University, College Station; **UAF**—University of Arkansas, Fayetteville; **UAT**—University of Arizona, Tucson; **UCB**—University of California, Berkeley; **UCD**—University of California, Davis; **UCR**—University of California, Riverside; **UGA**—University of Georgia, Athens; **UIM**—University of Idaho, Moscow; **UMAA**—University of Michigan, Ann Arbor; **UMC**—University of Missouri, Columbia; **UMSP**—University of Minnesota, St. Paul; **UNH**—University of New Hampshire, Durham; **USNM**—National Museum of Natural History, Washington, D.C.; **UWL**—University of Wyoming, Laramie; **UWM**—University of Wisconsin, Madison; **VPI**—Virginia Polytechnic Institute and State University, Blacksburg; **WSU**—Washington State University, Pullman.

Methods. Recent characterizations of *Sympherobius* species have relied heavily on male genital sclerites for specific diagnoses. Species treatments in this work include descriptions of diagnostic venational and genitalic features. These are supplemented by forewing photographs and figures of the male ectoproct, gonarcus and parameres. Geographic range maps are also provided for each species.

Male genitalia were prepared for dissection by clearing for 5 to 10 minutes in a sub-boiling solution of 10 percent NaOH. Cleared material was neutralized in dilute acetic acid, rinsed in water, dried on a paper blotter and transferred to glycerin for examination. A compound microscope was used to examine fine structural details of genital sclerites temporarily mounted in glycerin on depression slides.

To better illustrate important details of the parameres, gonarcus and ectoprocts,

these structures have been figured individually. Dorsal and/or lateral illustrations of the parameres (e.g., Figs. 10–11) and 'ninth tergite + ectoproct' (e.g., Fig. 8) of each species are shown in standard orientations with anterior to the left. Lateral views of the gonarcus (e.g., Fig. 9) have been rotated approximately 90 degrees clockwise to facilitate plate composition. In the species treatments relative positional descriptors of gonarcus regions (e.g., dorsal, anterolateral) refer to the gonarcus as figured, not as oriented *in situ*. The relative *in situ* positions of the male gonarcus and parameres are illustrated in Figure 2.

When interpreting illustrations of the gonarcus it should be remembered that the pseudomediuncus complex (Fig. 2, pm) articulates freely both with the apex of the gonopons (gpo) and at a second region of flexion located between the basipseudo- mediuncus (bpm) and distopseudomediuncus (dpm); the absolute positions of these structures will vary from specimen to specimen. Similarly, each ectoproct (Fig. 1, ect) articulates freely with the adjacent posterolateral margin of the ninth tergite (9t); the shape of the outline of the ectoproct, and its various processes, in lateral view will vary depending upon the absolute positions of these sclerites.

Forewing photographs were produced using Kodak Panatomic-X film from wings slide mounted in Hoyer's solution. Forewing lengths were measured from the anterior margin of the tegula to the wing apex. All drawings and measurements were made using a calibrated ocular grid reticle.

Detailed collection data and repository information are recorded only for the eight species for which fewer than 25 specimens have been examined. The corresponding data for the nine remaining species are summarized by recording for each: (1) geo- graphic distribution by country and state, (2) extremes of temporal occurrence taken from collection labels and (3) a list of institutional collections containing the species. More detailed collection data for these species have been compiled from collection labels and are available from the author upon request. Information recorded for each species under the heading *Distributions and Associations* has been compiled from data contained on specimen labels and from published sources.

Since female genital structures are inadequate for species diagnosis, and the fore- wing markings of some species exhibit overlapping ranges of variation, confident identification of females is sometimes not possible.

Geographical coverage. The primary geographic area addressed in this revision is North America north of Mexico (considered here for practicality to be synonymous with the Nearctic faunal region); however, all known extralimital records of Nearctic species are also noted. The species list in Appendix 1 and the listing of generic synonyms given at the beginning of the generic treatment are worldwide in scope.

TERMINOLOGY

Terms used for male and female genital structures are primarily those of Tjeder (1954, 1961, 1970). For descriptions and discussions of the several new terms pro- posed in this work for male genitalic structures see below under the heading *Ter- minology of Male Genital Sclerites.* The venational terminology used is primarily that of Carpenter (1940).

ABBREVIATIONS AND ANNOTATIONS

Abbreviations used for institutional collections are recorded above under the head- ing *Materials.* The following abbreviations and symbols have been used to annotate

papers cited in the synonymical listings given at the beginning of each species treat-
ment: A, adult description or characterization; Bic, biocontrol; Bio, biology; C, co-
coon; Dst, distribution; E, egg; F, female description or characterization; Key, key
or keyed; L#, larva, # indicates instar number; Lst, list or listed; Mg, male genitalia;
Mor, morphology (other than taxonomic characters); OD, original description; P,
pupa; Par, parasites; PP, prepupa; RD, redescription; Tax, taxonomy (including
synonymy, homonymy, type data, etc.); W, wing. An asterisk (*) following any of
the preceding abbreviations indicates a figure of the item it follows, e.g., FW* =
forewing figure.

SYMPHEROBIUS BANKS

Sympherobius Banks, 1904b:209 (Type species: *Hemerobius amiculus* Fitch, [1855]
    1854:799, by monotypy): Banks, 1905b (OD, Key); Banks, 1907b (Lst, Tax); Na-
    kahara, 1915 (RD, Lst, Tax); Comstock, 1918 (Mor); Krüger, 1922 (Tax); Kil-
    lington, 1936 (Bio, Mor); Killington, 1937 (RD, Key, Tax); Balduf, 1939 (Bio);
    Carpenter, 1940 (RD, Key, Tax); Kozhantshikov, 1956 (Key, Tax); Nakahara,
    1960 (RD, Lst, Tax); Tjeder, 1961 (RD, Key, Tax); Kuwayama, 1962 (Key, Tax);
    Stange, 1967 (Lst, Tax); Penny, [1978] 1977 (Lst, Tax); Aspöck et al., 1980 (RD,
    Key, Tax).
Spadobius Needham, 1905:16 (Type species: *Hemerobius occidentalis* Fitch, [1855]
    1854:799, by original designation, but see *Nomenclatural Note* below): Banks,
    1907b (Tax); Krüger, 1922 (Tax).
Palmobius Needham, 1905:17 (Type species: *Hemerobius amiculus* Fitch, [1855]
    1854:799, by original designation): Banks, 1907b (Tax).
Niremberge Navás, 1909:377 (Type species: *Niremberge limpida* Navás, 1909 [a
    junior subjective synonym of *Hemerobius fuscescens* Wallengren, 1863:22], by
    monotypy): Killington, 1937 (Tax); Aspöck et al., 1980 (Tax).
Coloma Navás, 1915c:129 (Type species: *Megalomus marmoratipennis* Blanchard
    in Gay, 1851:127, by original designation): Nakahara, 1960 (Tax).
Nefasitus Navás, 1915c:131 (Type species: *Sympherobius amicus* Navás in Silvestri,
    1915:332 [a junior subjective synonym of *Sympherobius fallax* Navás, 1908b:408],
    by original designation): Nakahara, 1960 (Tax); Aspöck et al., 1980 (Tax).
Lachlanius Krüger, 1922:171 (Type species: *Hemerobius inconspicuus* McLachlan,
    1868:177 [a junior subjective synonym of *Hemerobius fuscescens* Wallengren, 1863:
    22], by original designation): Killington, 1937 (Tax).
Eurobius Krüger, 1922:171 (Type species: *Hemerobius elegans* Stephens, 1836:113,
    by original designation): Killington, 1937 (Tax).
Sympheromima Kimmins, 1928:363 (Type species: *Sympheromima marginata* Kim-
    mins, 1928:363, by original designation): **New Synonym** (see *Synonymical Note*
    below).

Diagnosis. Sympherobius may be distinguished from all other Nearctic hemerobiid
genera by the following combination of forewing characters (Fig. 4): (1) forewing
radius with only 2 oblique branches ("radial sectors"), (2) recurrent humeral vein
present, and (3) forewing outer gradate series composed of only 4 (very rarely 3 or
5) crossveins.
    Description. The following description is based primarily on Nearctic species, many
of the extralimital species have not been examined.
    Head: Maxillary palp five segmented, ultimate segment subsegmented; labial palp

three segmented, ultimate segment subsegmented, palpimacula present, consisting of several small, parallel, recumbent setae lying in a shallow depression.

Forewing: length 3–7 mm; humeral crossvein (Fig. 4, h) recurrent and usually pectinately branched but in species with a very narrow costal area (e.g., *S. beameri*) indistinctly so or nearly simple; radius normally with two oblique branches, R4+5+MA and R2+3 (very rarely one, Fig. 104, or three, Figs. 105–106); four crossveins (Fig. 4, og) in the outer gradate series (rarely three or five); proximal radial crossvein (Fig. 4, prc) present or absent; distal radial crossvein (Fig. 4, drc) present or absent; some setae of the longitudinal veins may be set within individual 'setal spots' (spots of darkly tanned cuticle encircling the bases of the setae).

Male terminalia: Tergite nine (Fig. 1, 9t): antecosta prominent; ventral surface along dorsal midline with a prominent costa; lateroventral margins produced posteroventrally as narrow processes which subtend the ectoprocts; anterodorsal margin frequently emarginate in dorsal view. Ectoprocts (Fig. 1, ect): bearing one (e.g., Fig. 8), two (e.g., Fig. 48) or three (e.g., Fig. 1) digitiform process(es) (Fig. 1, dlp, vlp, vmp) of varying length and curvature, each digitiform process bears at or near its apex one (e.g., Fig. 7) or two (e.g., Fig. 68) peg-like or spinose modified macrotrichia; 'dorsomedial prominence' (e.g., Figs. 56–57) present or absent; trichobothria of calli cercorum (Fig. 1, cc) with internally rosettiform alveoli. Gonarcus (Fig. 2): composed of a pair of lateral hemigonarcus (hg) oriented symmetrically about the gonopons (gpo); hemigonarcus with well-developed longitudinally oriented gonopleura (glp); gonoplakes (e.g., Fig. 89, gpx) variously but only weakly developed; pseudomediuncus (Fig. 2, pm) present, bipartite; mediuncus-arcessus absent; hemigonarcal (hgr) ribs present or absent. Parameres (Fig. 2): apophysis proxima (ap) elongate, compressed; apophysis proxima cavity (apc) present; one or more pairs of terminal lobes (mlp, llp) present. Hypandrium internum: a small wedge shaped sclerite with truncate or emarginate apex and revolute lateral margins.

Female terminalia (Fig. 3): Tergite eight (8t): lateral ends widely separated, adjacent or fused ventrally. Tergite nine (9t): expanded ventrally, prominent antecosta and middorsal costa of males absent. Gonapophyses laterales (gl): reniform, styli present. Gonapophyses posteriores: absent. Subgenitale a small oval or subrectangular plate, posterior margin sometimes emarginate. Seminal receptacle a darkly tanned sac or tube, ducts variously convoluted, seminal duct long and well sclerotized.

Terminology of male genital sclerites. Most of the terms coined by Tjeder (1954, 1970) for the male and female genital structures of neuropterous insects have been widely accepted and adopted by later neuropterists. Many of Tjeder's terms are applicable to *Sympherobius*. However, for the sake of clarity and precision, a number of new terms are proposed. These are given below, together with descriptions and justifications for each.

Ectoprocts: The digitiform processes of the ectoprocts have been designated as follows (Fig. 1): (1) ventromedial (vmp), (2) ventrolateral (vlp) and (3) dorsolateral (dlp), in reference to the relative positions of their points of insertion on the ectoproct. In like manner, a fourth process, shorter than the digitiform processes and not terminated by a modified macrotrichia (Figs. 56–57), has been designated the dorsomedial prominence. For additional discussion of the processes of the male ectoproct see Character 7 under the heading PHYLOGENETIC RELATIONSHIPS below.

Gonarcus: For descriptive purposes the neuropterous gonarcus is usually divided
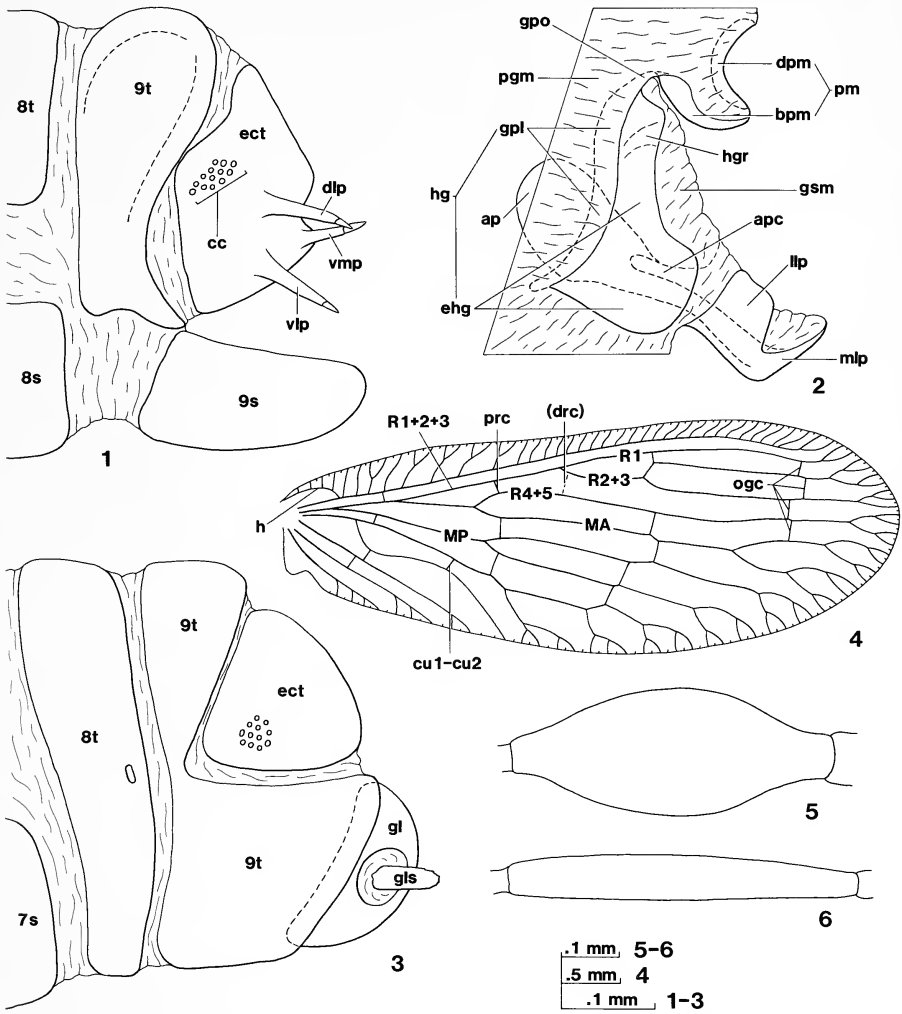
Figs. 1–6. *Sympherobius amiculus.* 1. Apex of male abdomen, lateral view. 2. *in situ* arrangement of male gonarcus, parameres and adjoining membranes, lateral view with overlaying sclerites removed. 3. Apex of female abdomen, lateral view. *S. angustus.* 4. Forewing, the usual position of distal radial crossvein (drc), which is absent in *S. angustus,* is shown as a dashed line. *S. pictus.* 5. Male protibia. *S. killingtoni.* 6. Male protibia. Abbreviations: ap, apophysis proxima; apc, apophysis proxima cavity; bpm, basipseudomediuncus; cc, callus cercus; cu1–cu2, cubital crossvein; dlp, dorsolateral ectoproct process; dpm, distopseudomediuncus; drc, distal radial crossvein; ect, ectoproct; ehg, extrahemigonarcus; gl, gonapophysis lateralis; gls, gonapophysis lateralis stylus; gpl, gonopleuron; gpo, gonopons; gsm, gonosaccal membrane; hc, humeral crossvein; hg, hemigonarcus; hgr, hemigonarcal rib; llp, lateral lobe of parameres; MA, media anteior; mlp, median lobe of parameres; MP, media posterior; ogc, outer gradate crossveins; pgm, paragonarcal membranae; pm, pseudomediuncus; prc, proximal radial crossvein; R#, radial veins; #s, sternites; #t, tergites; vlp, ventrolateral ectoproct process; vmp, ventromedial ectoproct process.

into a pair of laterally oriented, usually bilaterally symmetrical, gonarcus "wings," which are almost universally joined by a transverse dorsal bar or plate termed the gonarcus "bridge." For the "wing" and "bridge" of the gonarcus I propose, respectively, the terms *hemigonarcus* (Fig. 2, hg; name from the Greek "hemisys," half, and gonarcus; nominative plural = hemigonarcus) and *gonopons* (Fig. 2, gpo; name formed by elision and compounding of "gonarcus" and the Latin "pons," bridge; nominative plural = gonopontes). Relative to the terms gonarcus "wings" and gonarcus "bridge," the new terms hemigonarcus and gonopons, while remaining adequately descriptive, have the advantages of conciseness, euphony and classical derivation. These terms should be widely applicable to neuropterous gonarcus. In some species of *Sympherobius* the hemigonarcus possess darkened, obliquely or transversely oriented elongate tumosities near the gonopons. I term these structures the *hemigonarcal ribs* (Figs. 2, 89, hgr).

I also distinguish between the externally exposed region of the gonarcus, the *extragonarcus* (name from the Latin "exterus," out, and gonarcus; nominative plural = extragonarcus), and its adjacent internally projecting margin (apodeme), the *intragonarcus* (name from the Latin "intra-," within, and gonarcus; nominative plural = intragonarcus). These regions are delimited by the line of attachment to the hemigonarcus of the *paragonarcal membrane* (Fig. 2, pgm; name from the Greek "para-," near or by, and gonarcus; nominative plural = paragonarcal membranes), the anterior membrane attaching around the outside of the gonarcus, the posterior membrane attaching to the gonarcus being the *gonosaccal membrane* (gsm). The terms *intrahemigonarcus* (Fig. 89, ihg) and *extrahemigonarcus* (Figs. 2, 89, ehg) may be used to refer to the internal and external divisions, respectively, of a single hemigonarcus. In *Sympherobius* much of the extragonarcus is only lightly sclerotized and lightly tanned. Because of this, the boundary between the extragonarcus and adjacent gonosaccal membrane is not always distinct, and the shapes of the extrahemigonarcus may be somewhat variable.

Since hemerobiid genera vary greatly in their relative development of the intra- and extragonarcus, differentiation and identification of these regions should prove useful in discussions of hemerobiid genitalic morphology. As membranous attachments to the gonarcus have seldom been figured in prior works on the Hemerobiidae, this variation may not be readily apparent from an examination of those works.

In *Sympherobius, Nomerobius, Neosympherobius* and some other hemerobiid genera each intrahemigonarcus is composed of two more or less distinct regions which I term the *gonopleuron* (Fig. 89, gpl; name formed by elision and compounding of "gonarcus" and the Greek "pleuron," rib; nominative plural = gonopleura) and the *gonoplax* (Fig. 89, gpx; name formed by elision and compounding of "gonarcus" and the Greek "plax," anything flat and wide; nominative plural = gonoplakes). The gonopleura (Fig. 2) are elongate thickened regions of the hemigonarcus which lie adjacent, internally, to the line of attachment of the paragonarcal membrane. The gonopleura apparently function as supportive mechanical struts for the hemigonarcus and probably also as sites for muscular attachments. The gonoplakes are thin, sclerotized processes of the gonopleura. These spiniform, cariniform or lamellate structures project into the body cavity from the internal margins of the gonopleura and exhibit considerable intra- and interspecific variation in shape. These structures almost certainly serve as sites for muscle attachments.

Pseudomediuncus: The sclerotized posteromedian process of the gonarcus in *Sympherobius* has been termed the aedeagus (Killington, 1937:112; Carpenter, 1940:229; Nakahara, 1960:15) the arcessus + mediuncus (Tjeder, 1939:27) or simply the arcessus (Tjeder, 1961:342). Detailed examination of this organ has revealed that it is not a homologue of the structure usually given the term mediuncus or arcessus in other Neuroptera by Tjeder and subsequent authors. Rather, it is a separate sclerotized region lying along the dorsal midline of the paragonarcal membrane immediately adjacent to and continuous with the gonopons. I name this organ the *pseudomediuncus* (Fig. 2, pm; from the Greek "pseudos," fallacy or lie, and mediuncus; nominative plural = pseudomediunci).

The pseudomediuncus is confluent with the gonarcus at the posterior margin of the gonopons. This arrangement might be expected of either a sclerite developed in the adjacent paragonarcal membrane or a homologue of the normally medially situated mediuncus-arcessus of other Neuroptera. However, two lines of evidence strongly suggest that the pseudomediuncus is not a homologue of the mediuncus-arcessus: (1) the membranes contiguous with the lateral margins of the pseudomediuncus are confluent with the paragonarcal membrane, not the gonosaccal membrane as would be expected for the mediuncus-arcessus homologue (in *Sympherobius* the gonosaccal membrane is continuous with the posterior margin of the extragonarcus and terminates on the ventral surface of the gonopons near the base of the pseudomediuncus, Fig. 2) and (2) species of the South American genus *Nomerobius* possess not only a pseudomediuncus but also a structure which is apparently a homologue of the mediuncus of other Neuroptera. This structure is composed of a pair of narrow, laterally adjacent, lobes which insert on the venter of the gonopons. The membranes attaching to the bases of these lobes are confluent with the gonosaccal membrane. This membranous attachment, together with the position of the lobes, suggests that these structures may be mediuncus homologues. A third genus known to possess a pseudomediuncus, *Neosympherobius,* lacks recognizable mediuncus homologues.

The pseudomediunci of *Nomerobius* and *Neosympherobius* consist of narrow, undivided, weakly sclerotized and weakly tanned strips of cuticle lying longitudinally along the midline of the paragonarcal membrane. In *Sympherobius* the pseudomediuncus is composed of a pair of sclerites, a proximal *basipseudomediuncus* (Fig. 2, bpm) and a distal *distopseudomediuncus* (dpm). These sclerites are joined at a narrowed joint or region of articulation which may be membranous or weakly sclerotized. The lateral margins of the basipseudomediuncus are splayed and recurved forming a shallow basin into which, by articulation at the intervening joint, the distopseudomediuncus may loosely seat. In *Sympherobius* the pseudomediuncus complex articulates with the posterior apex of the gonopons and frequently hangs down between or slightly posterior to the hemigonarcus. When thus situated it occupies a position filled by the mediuncus in most Neuroptera and thereby adds to the illusion of homology between itself and the true mediuncus-arcessus.

Parameres (Fig. 2): In *Sympherobius* the parameres are composed of a spathulate apodeme called the *apophysis proxima* (ap), and one, two or three pairs of terminal lobes (the median [mlp], lateral [llp] and anterior lobes [Fig. 26, alp]) which are arranged in bilateral symmetry about the plane of the apophysis proxima (Fig. 87). At its base, the apophysis proxima encloses a compressed cavity here called the *apophysis proxima cavity* (Fig. 2, apc). The apophysis proxima itself is a prominent

apodeme which projects for a considerable distance into the body cavity. Diverse configurations of the terminal lobes of the parameres result from differential patterns of sclerotization of the arthrodial membrane located primarily ventral and posterior to the external opening of the apophysis proxima cavity. The margins of the terminal lobes are sometimes not sharply delimited at their boundaries with adjacent unsclerotized membrane.

The innermost pair of terminal lobes, the median lobes ["distal lobes" of Nakahara (1965a)], are present in all species. The inner margins of the median lobes (Fig. 87) are adjoined basally along a line continuous with the longitudinal midline of the apophysis proxima. Distally the median lobes are separated by an emargination of variable shape and depth. The lateral lobes (Fig. 87) ["lateral flaps" of Nakahara (1965a)], when present, arise from the anterolateral margins of the median lobes. The ventral surfaces of the median and lateral lobes are minutely spinulate. The margins of these lobes may be finely or coarsely toothed. The anterior lobes (Fig. 26) ["oblique process" of Carpenter (1940), "middle arm" of Gurney (1948) and others], when present, arise from the anterior margin of the median lobes. The anterior lobes project dorsally and may have simple or expanded apices.

Immature stages. The preadult stages and biology of *Sympherobius* species are poorly known. Some immature stages of *S. amiculus, S. barberi* and *S. californicus* [as *S. angustus*] have been described by Smith (1923), Smith (1934) and Essig (1910) respectively. Additional descriptions and/or figures of some immature stages of one or more non-Nearctic species are found in the following works: Killington (1931, 1937), New (1967a, b), Withycombe (1923) and Yang (1980). Known larvae and adults are predaceous on small invertebrates. As inferred from published prey records, preferred prey are apparently various sternorrhynchous Homoptera, particularly pseudococcids.

Distribution. The genus *Sympherobius* is widely distributed throughout the temperate and tropical regions of North and South America and Europe, and the nontropical regions of Africa and Asia. Species have not been reported from tropical Africa, the Oriental or the Australasian faunal regions. The approximate distribution of each world species is given in Appendix 1.

In America north of Mexico, *Sympherobius* ranges north only to extreme southern Canada with its highest diversity found in the arid regions of the southwestern United States. The ranges of many Nearctic species extend south through Mexico. One species, *S. barberi,* has been recorded as far south as Peru. No species are Holarctic in distribution.

Etymology. Banks did not give the etymology of the name *Sympherobius*; however, it is almost certainly derived from the Greek "sympheron," useful, probably in reference to the beneficial predatory habits of the larvae and adults. Gender: masculine.

Synonymical note. Kimmins (1928:363) based his description of *Sympheromima marginata,* and the monobasic genus *Sympheromima,* on a single specimen lacking an abdomen collected at Cerro Zunil, Guatemala. None of the characters cited in the generic description, except possibly the slightly falcate posterodistal margin of the forewing, are adequate to distinguish *Sympheromima* from *Sympherobius.* The cited two oblique branches of the forewing radius, few crossveins of the forewing outer gradate series, and other venational characters are identical, or nearly so, with states found in *Sympherobius.*

Recently, a single specimen strongly agreeing with Kimmins' original description of the coloration and venation of the forewing of *Sympheromima marginata* was found in the collection of the National Museum of Natural History (Data—Mexico: Veracruz: near Huatusco; 25/26-VII-1965; Flint and Ortiz). This specimen is apparently the first known male of *Sympheromima marginata.* The ectoprocts of this specimen each bear three digitiform processes, each terminating in a peg-like seta as in many *Sympherobius.* Furthermore, *Sympheromima marginata* possesses the two synapomorphies of *Sympherobius*: (1) a bipartite pseudomediuncus and (2) a laterally expanded basipseudomediuncus. Based on the presence of the ventromedial, ventrolateral and dorsolateral ectoproct processes, *Sympheromima marginata* would join the cladogram for Nearctic *Sympherobius* (Fig. 114) at some point distal to the position of Character 7 (absence-presence of the dorsolateral ectoproct process), a point well removed from the base of the *Sympherobius* clade.

The above characters, together with the fact that continued recognition of *Sympheromima* would render *Sympherobius* paraphyletic, justify the placement of *Sympheromima* as a junior subjective synonym of *Sympherobius.*

Nomenclatural note. The generic name *Spadobius* appears to have been based on a specimen of *Sympherobius amiculus* misidentified as *Sympherobius occidentalis* (see Carpenter, 1940:227). This is a case of misidentified type species which should be referred to the International Commission on Zoological Nomenclature for type selection under Article 70 of the International Code of Zoological Nomenclature (1985). However, since *S. amiculus* and *S. occidentalis* have been considered congeneric by all authors subsequent to the proposal of the generic name *Spadobius* in 1905 (except Krüger, 1922), nomenclatorial stability is not presently threatened by this misidentification; and submission of this case to the Commission is unnecessary at the present time.

Classification. The following suggested classification of the Nearctic species of *Sympherobius* is based on clades derived from the cladistic analysis presented below. Subsequent inclusion of extralimital species may require revision of the preliminary groupings proposed here.

CLASSIFICATION OF NEARCTIC *SYMPHEROBIUS*

S. perparvus species group
  S. perparvus (McLachlan, 1869)
  S. beameri Gurney, 1948
  S. arizonicus Banks, 1911
  S. killingtoni Carpenter, 1940
S. pictus species group
  S. pictus (Banks, 1904)
  S. similis Carpenter, 1940
  S. occidentalis (Fitch, [1855] 1854)
  S. limbus Carpenter, 1940
  S. distinctus Carpenter, 1940
  S. angustus complex
    S. angustus (Banks, 1904)
    S. quadricuspis n. sp.

S. bifasciatus Banks, 1911
S. californicus Banks, 1911
S. constrictus n. sp.
S. barberi complex
   S. barberi (Banks, 1903)
   S. umbratus (Banks, 1903)
   S. amiculus (Fitch, [1855] 1854)

Comment on the classification of European Sympherobius. Aspöck et al. (1980) advocated recognition of the subgeneric name *Sympherobius* (*Niremberge*) for the four European species *S. fuscescens, S. klapaleki, S. pellucidus* and *S. riudori*; the three other European species of *Sympherobius, S. pygmaeus, S. elegans* and *S. fallax* were retained in the nominate subgenus *Sympherobius* (*Sympherobius*). Two putative derived characters seem to support the hypothesis that the first four species form a group distinct from the other European species: (1) the forewing usually possesses three (not two) oblique radial branches and (2) the ventrolateral digitiform process of the male ectoproct bears two (not one) modified peg-like apical setae. These four species also lack lateral lobes on the parameres, and have only two digitiform processes on the male ectoproct. Given this distribution of characters, a lineage comprised of these species would join the cladogram in Figure 114 at a point between *S. pictus* and *S. limbus* (i.e., above character 3 [presence of the ventrolateral ectoproct process] but below character 7 [presence of the dorsolateral ectoproct process]). It is clear that classification of these species in a subgenus *Niremberge* would render paraphyletic the nominate subgenus containing all North American and the remaining European species. For this reason, I do not accept the retention of *Niremberge* as a subgenus.

If differentiation of the four species placed by Aspöck et al. (1980) in the subgenus *Niremberge* is desirable as an initial estimation of intrageneric relationships within the European *Sympherobius* fauna, I suggest that use of an informal designation such as the "*fuscescens* species group" be employed. Deferment of formal nomenclatural designation of such a group is desirable until, through increased documentation of intrageneric relationships worldwide, this genus can be comprehensively divided into monophyletic subunits.

<div align="center">

KEY TO ADULT *SYMPHEROBIUS* OF
AMERICA NORTH OF MEXICO

</div>

Couplets 2 through 16 of the following key primarily utilize forewing characteristics, couplets 17 through 32 utilize characters of the male genitalia. While color and maculation patterns of the forewing are valuable identification aids and, with some practice, are adequate to identify most species, these characters are subject to considerable intraspecific variation which cannot be efficiently represented in a dichotomous key. For this reason, use of the genitalic portion of the key, and its associated figures, is recommended for maximum accuracy in making identifications. Though positive identification of females is sometimes problematic, females of most species can be identified with reasonable confidence using forewing characters or by association with known males. Five species cannot be confidently keyed using forewing characters. In the forewing section of the following key, couplets leading to these

species are referred directly to the appropriate couplet of the genitalic portion of the key.

14(13').   Maculations of diffuse yellowish brown, margins of maculations poorly de-
             fined, setal spotting of longitudinal veins weak .... *S. limbus* (Fig. 21)
14'.   Maculations light or dark brown with irregular though usually relatively dis-
             tinct margins, setal spotting of longitudinal veins usually prominent (Figs.
             17–20) .... *S. arizonicus, S. killingtoni* 31
15(12).   Membrane hyaline with scattered brownish maculations, especially around the
             inner gradate crossveins and forks of the radial veins ...... *S. perparvus* (Fig. 65)
15'.   Membrane hyaline, immaculate .... *S. beameri*
16(1').   Ectoprocts: 1 (e.g., Fig. 8) or 2 (e.g., Fig. 48) digitiform process(es) present;
             each process with only a single modified terminal seta; dorsomedial promi-
             nence absent 21
16'.   Ectoprocts: 3 digitiform processes present (e.g., Fig. 1); ventrolateral process
             with one (e.g., Figs. 92, 97) or two (Figs. 68, 108) modified terminal seta(e);
             dorsomedial prominence present (Figs. 57, 72) or absent 17
17(8,16').   Ectoprocts: dorsomedial prominence absent 18
17'.   Ectoprocts: dorsomedial prominence present 24
18(17).   Ectoprocts: ventrolateral process with two modified terminal setae (Figs. 68,
             108) 25
18'.   Ectoprocts: ventrolateral process with one modified terminal seta (e.g., Figs.
             92, 97) 19
19(18').   Parameres: lateral lobes present (e.g., Figs. 58, 87) 20
19'.   Parameres: lateral lobes absent (e.g., Figs. 37, 41) 26
20(19).   Parameres: emargination separating median from lateral lobes deep and nar-
             row in dorsal view (Figs. 87, 93) 27
20'.   Parameres: emargination dividing median and lateral lobes absent or broad
             in dorsal view (Figs. 83, 98) 28
21(16).   Ectoprocts: 1 digitiform process present 22
21'.   Ectoprocts: 2 digitiform processes present 29
22(21).   Parameres: anterior lobes present (e.g., Figs. 10, 26); Ectoproct: ventromedial
             process less than twice as long as its modified terminal seta (e.g., Figs. 8, 24),
             calyx of setal socket produced into an elongate tubular sheath (e.g., Figs. 7,
             23) 23
22'.   Parameres: anterior lobes absent (Fig. 37); Ectoproct: ventromedial process
             much more than twice as long as its modified terminal seta (Fig. 36), calyx
             of setal socket not produced into an elongate tubular sheath .... *S. pictus*
23(22).   Parameres: apices of anterior lobes expanded (Figs. 10, 15); Ectoproct: ven-
             tromedial surface of modified seta not impressed (Figs. 7, 12) 30
23'.   Parameres: apices of anterior lobes not expanded (Figs. 26, 31); Ectoproct:
             ventromedial surface of modified seta impressed (Figs. 23, 28) 31
24(17').   Parameres: apices of median and lateral lobes acute, margins with large teeth,
             emargination dividing median lobes deep and U-shaped (Fig. 73) ....
             ....*S. quadricuspis*
24'.   Parameres: apices of lateral lobes broadly rounded, margins without large
             teeth, emargination dividing median lobes shallow and V-shaped (Fig. 58)
             .... *S. angustus*
25(18).   Parameres: margins of median lobes with large teeth (Fig. 69); Ectoprocts:
             ventrolateral process short and deeply divided (Fig. 68) .... *S. bifasciatus*
25'.   Parameres: margins of median lobes without large teeth (Fig. 110); Ectoprocts:
             ventrolateral process long and only shallowly divided (Fig. 108) ... *S. umbratus*
26(19').   Parameres: posterior margin of median lobes with distinct teeth (Fig. 45);
             Gonarcus: anterior portion of gonopleuron deflexed (Fig. 47) ....*S. limbus*

26'.   Parameres: posterior margin of median lobes without distinct teeth (Fig. 53);
              Gonarcus: anterior portion of gonopleuron not deflexed (Fig. 55) .. *S. distinctus*
27(20).   Parameres: lateral lobes subtriangular, posterior margins toothed, longitudinal
              ridge present (Fig. 87) .... *S. californicus*
27'.   Parameres: lateral lobes elongate-oval, apices reflexed, margins without teeth,
              ridge absent (Fig. 93) .... *S. barberi*
28(20').   Parameres: lateral lobes supported by a thickened rod, margins toothed (Fig.
              83) .... *S. constrictus*
28'.   Parameres: lateral lobes not supported by a thickened rod, margins not toothed
              (Fig. 98) .... *S. amiculus*
29(21').   Parameres: anterior lobes present, apical margins of median lobes toothed
              (Fig. 49) .... *S. occidentalis*
29'.   Parameres: anterior lobes absent, apical margins of median lobes not toothed
              (Fig. 41) ....*S. similis*
30(23).   Ectoproct: ventromedial process, excluding calyx sheath, distinctly free of
              ectoproct, process curved ventromedially (Fig. 8), calyx sheath tightly con-
              stricting modified seta (Fig. 7) .... *S. perparvus*
30'.   Ectoproct: ventromedial process, excluding calyx sheath, short and indistinct,
              process directed posterodorsally (Fig. 13), calyx sheath loosely encircling mod-
              ified seta (Fig. 12) .... *S. beameri*
31(14',23'). Ectoproct: modified seta terminating a short recumbent process, base of pro-
              cess produced internally as a short apodeme (Fig. 29), calyx sheath tightly
              constricting modified seta (Fig. 28); Gonarcus: gonopleuron produced well
              beyond anterior margin of extrahemigonarcus (Fig. 30) .... *S. arizonicus*
31'.   Ectoproct: modified seta terminating a short, free-standing process, base of
              process not produced internally (Fig. 24), calyx sheath loosely encircling mod-
              ified seta (Fig. 23); Gonarcus: gonopleuron ending nearly even with anterior
              margin of extrahemigonarcus (Fig. 25) .... *S. killingtoni*

SYMPHEROBIUS PERPARVUS SPECIES GROUP

Sympherobius perparvus (McLachlan)
Figs. 7–11, 65, 112

Hemerobius perparvus McLachlan, 1869:22 (OD, A). Lectotype male. UNITED
   STATES: Texas: Bosque Co. (BMNH, by present designation, see *Type material
   examined* below): Banks, 1892 (Lst); Banks, 1903 (MG*, Dst); Banks, 1904a (Dst);
   McClendon, 1906 (Dst).
Sympherobius perparvus (McLachlan): Banks, 1905b (RD, A, MG*, Dst, Key, Lst);
   Banks, 1907b (Lst); Banks, 1911 (Key); Smith, 1925 (Dst); Smith, 1934 (Dst, Key);
   Carpenter, 1940 (RD, A, MG*, W*, Dst, Key, Tax); Gurney, 1948 (MG*, Key);
   Nakahara, 1960 (Dst, Tax); Nakahara, 1965a (Dst).
Sympherobius sparsus Banks, 1911:346 (OD, A, Key). Holotype female. UNITED
   STATES: Kansas: [Douglas Co. ?] (MCZ type #11,489): Smith, 1925 (Dst); Smith,
   1934 (Dst, Key); Carpenter, 1940 (Tax).
Eurobius perparvus (McLachlan): Krüger, 1922 (Tax).

Description. Antennae: Ochraceous to brown, usually darker distally. Forewing
(Fig. 65): Length 3.20–4.63 mm ($\bar{x} = 3.77$, N = 25). Longitudinal veins hyaline to
ochraceous, concolorous; setal spotting weak or absent; gradate crossveins light brown,
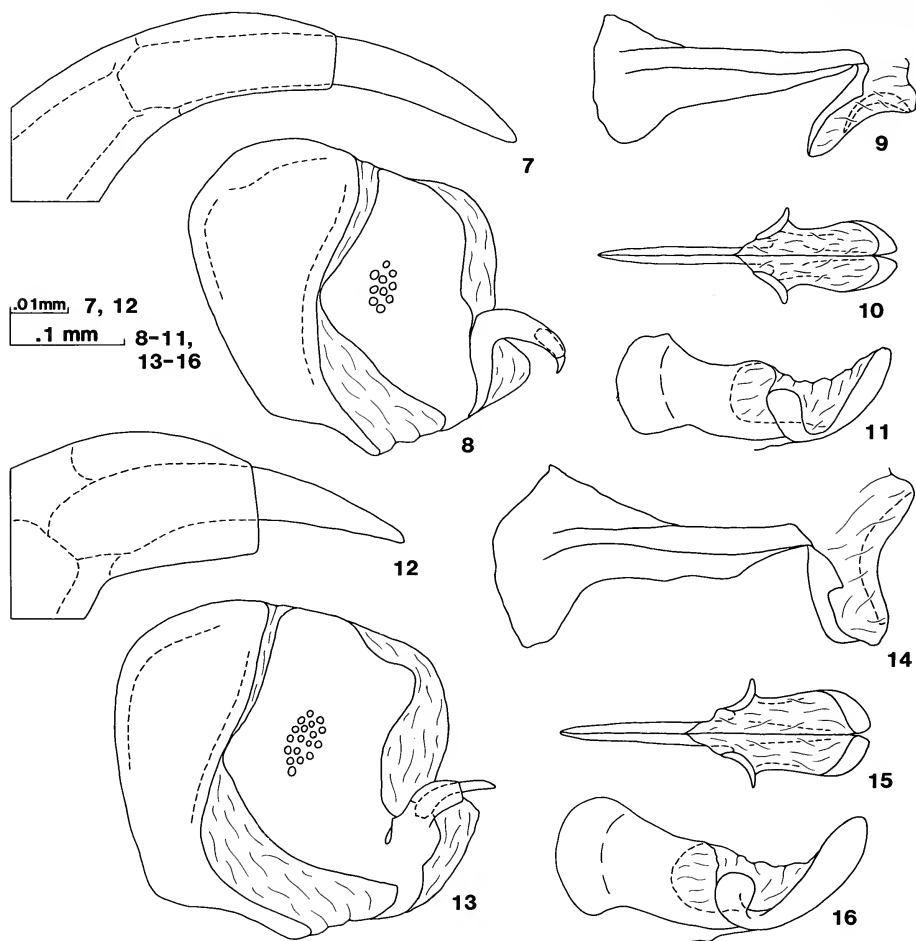
Figs. 7–16. *Sympherobius perparvus*. 7. Apex of ventromedial ectoproct process. 8. Ninth tergite and ectoproct, lateral. 9. Gonarcus, lateral. 10–11. Parameres, dorsal and lateral. *S. beameri*. 12. Apex of ventromedial ectoproct process. 13. Ninth tergite and ectoproct, lateral. 14. Gonarcus, lateral. 15–16. Parameres, dorsal and lateral.

margined with light brown; membrane hyaline with scattered light brown spotting, particularly in distal forks of longitudinal veins; proximal and distal radial crossveins absent.

Male genitalia: Ectoprocts (Figs. 7, 8): One elongate unisetose process present; calyx of setal socket produced into a tubular sheath constricting base of seta; process and terminal modified seta curved ventromedially; seta slightly longer than process excluding sheath; ventromedial surface of seta not impressed. Hemigonarcus (Fig. 9): Gonopleuron linear; gonoplax a small, triangular, anterodorsal plate; extrahemigonarcus lobate anteriorly, narrowed posteriorly; hemigonarcal rib absent. Parameres

(Figs. 9, 10): Apices of median lobes reflexed; lateral lobes absent; anterior lobes large, curved dorsally, apices expanded; apophysis proxima broad.

Remarks. For a discussion of similar species see *Remarks* under *S. killingtoni.*

Distributions and associations. Geographic distribution (Fig. 112): Central and western United States and northern Mexico. Temporal distribution: 21 March through 15 October. Altitudinal distribution: 270'–6,400' (82 m–1,951 m). Plant associations: Pine-Oak zone (southern Arizona).

Type material examined. Hemerobius perparvus McLachlan. Lectotype male by present designation. Verbatim label data: "type," "20/9," "type," "Bosque Co. / Texas / Belfrage," "McLachlan Coll. / B.M. 1938-674," "Hemerobius / perparvus / McL.," "Lectotype / Hemerobius / perparvus / McLachlan, 1869 / Oswald, 1985." Condition: excellent, complete. Right wings pinned below specimen between two cover slips. One male paralectotype, same data as lectotype (BMNH). Only two specimens of the type series of *S. perparvus* are presently in the British Museum of Natural History (P. C. Barnard, pers. comm.). Three specimens were mentioned by McLachlan (1869) in the original description of *S. perparvus.* The third specimen is presumed lost. The two syntypes which I have examined are both males. Carpenter (1940) indicates incorrectly that the type series contains two females and one male. Each of the two specimens examined has been labeled "type" and/or "paratype" sometime in the past, but no primary type designation has been published for *S. perparvus.* I have selected and clearly labeled the better of the two specimens as the lectotype.

Hemerobius sparsus Banks. Holotype female. Verbatim label data: "type," "Kans.," "Collection / N. Banks," "Type / 11489," "Sympherobius / sparsus / type Bks." Condition: abdomen and tips of antennae missing, body and hindwings damaged by museum pests, otherwise complete.

Other material examined. 139 specimens. MEXICO: Baja California Sur, Chihuahua, Coahuila; UNITED STATES: Arizona, California, Colorado, Iowa, Kansas, Minnesota, Montana, Nebraska, New Mexico, Nevada, Oklahoma, Oregon, South Dakota, Texas, Utah, Wyoming. Institutions: ASUT, BMNH, CAS, CU, ISU, MCZ, MSU, OKS, OSUC, SMEK, TAMU, UAT, UCB, UCD, UCR, UIM, UMSP, USNM, UWL. Also recorded from UNITED STATES: New York (Nakahara, 1960). This questionable record has not been confirmed.

<div align="center">

Sympherobius beameri Gurney
Figs. 12–16, 33

</div>

Sympherobius beameri Gurney, 1948:220 (OD, A, MG*, W*, Key). Holotype male. UNITED STATES: California: El Dorado or Placer Co., Lake Tahoe (SMEK): Nakahara, 1965a (Dst).

Description. Flagellum light to medium brown, apices usually darker. Forewing: Length 3.64–4.39 mm ($\bar{x} = 3.96$, N = 7). Longitudinal veins and crossveins hyaline, not margined with brown; setal spotting absent; membrane hyaline, immaculate or nearly so; proximal and distal radial crossveins absent.

Male genitalia: Ectoprocts (Figs. 12, 13): One short, unisetose process present; calyx produced into a tubular sheath loosely encircling base of seta; seta short and arcuate, directed posterodorsally, ventromedial surface not impressed. Hemigonarcus
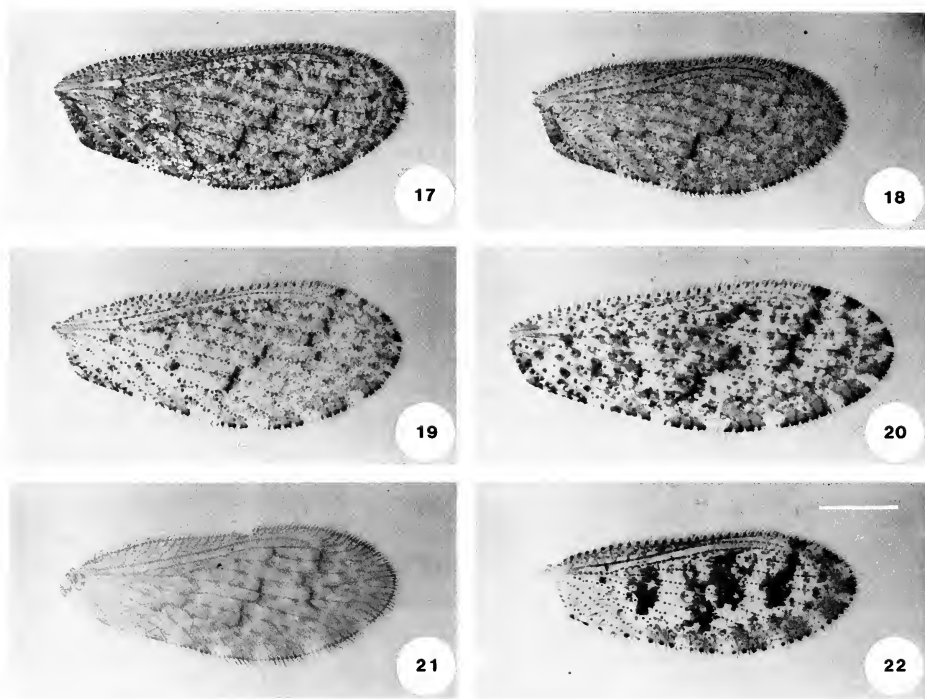
Figs. 17–22.   Forewings of *Sympherobius*. 17. *S. arizonicus*. 18–20. *S. killingtoni*. 21. *S. limbus*. 22. *S. pictus*. Scale bar = 1 mm. All figures to same scale.

(Fig. 14): Gonopleuron linear; gonoplax a triangular anterodorsal plate; extrahemigonarcus broad anteriorly, narrowed posteriorly; hemigonarcal rib absent. Parameres (Figs. 15, 16): Apices of median lobes reflexed; lateral lobes absent; anterior lobes present, curved dorsally, apices expanded; apophysis proxima broad.

Remarks. The forewing of *S. beameri* is similar to that of *S. perparvus* (Fig. 65), but immaculate. The male genitalia are also similar to *S. perparvus* but may be distinguished by the short ectoproct process.

Distributions and associations. Geographic distribution (Fig. 33): Southwestern United States. Temporal distribution: 28 May through 10 September. Altitudinal distribution: 3,050'–7,500' (930 m–2,286 m). Plant associations: no records.

Primary type material examined. Sympherobius beameri Gurney. Holotype male. Verbatim label data: "Lake Tahoe Calif / VIII 11-40 / R.H. Beame[r]," "Sympherobius / beameri / Gurney / Type." Condition: good, tips of antennae and several tarsal segments missing, otherwise complete. Genitalia in glycerin in microvial pinned below specimen.

Other material examined. 13 specimens. UNITED STATES: Arizona: Cochise Co.: S.W. Research Station, 5 mi SW Portal, 23.v.–5.vi.1967 (USNM). Graham Co.: Aravaipa Cyn., 24.viii.1976 (UAT). Maricopa Co.: Phoenix, 10.ix.1945 (UCR). Pima or Pinal Co.: Santa Catalina Mts., 28.v.1933 (CAS). California: Inyo Co.: Bishop, 3 specimens, 20–21.vi.1929 (CAS); Little Lake, 7.vi.1929 (CAS); Lone Pine, 28.vii.1940
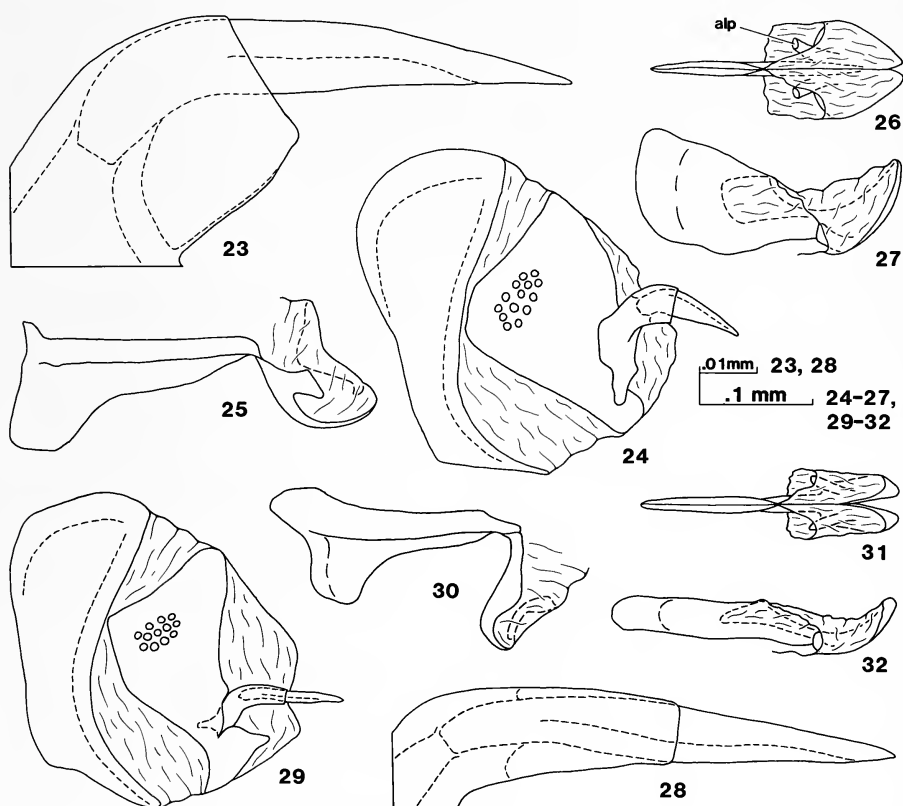
Figs. 23–32. *Sympherobius killingtoni.* 23. Apex of ventromedial ectoproct process. 24. Ninth tergite and ectoproct, lateral. 25. Gonarcus, lateral. 26–27. Parameres, dorsal and lateral. *S. arizonicus.* 28. Apex of ventromedial ectoproct process. 29. Ninth tergite and ectoproct, lateral. 30. Gonarcus, lateral. 31–32. Parameres, dorsal and lateral. Abbreviations: alp, anterior lobe of parameres.

(SMEK); Lone Pine, Diaz Lake., 14.vi.1972 (UCR). Kern Co.: Rosamond, 2 specimens, 23.vii.1940 (SMEK, USNM). Utah: Salt Lake Co.: Saltair, 12.vii.1922 (CAS).

Sympherobius arizonicus Banks
Figs. 17, 28–32, 33

Sympherobius arizonicus Banks, 1911:346 (OD, A, Key). Holotype female. UNITED STATES: Arizona: Yavapai Co., Prescott (MCZ type #11,468): Carpenter, 1940 (RD, A, W*, Dst, Key); MacLeod, 1963 (RD, A, MG*); Nakahara, 1965b (Dst).

Description. Antennae: Dark Brown. Forewing (Fig. 17): Length 2.94–5.10 mm ($\bar{x}$ = 4.03, N = 25). Longitudinal veins hyaline with prominent setal spotting; gradate crossveins brown and margined with brown; membrane densely covered with brown maculations broken by hyaline regions or spots; maculations particularly dense along

distal and posterodistal border of wing; margin in these regions broken only by short hyaline areas; proximal and distal radial crossveins absent.

Male genitalia: Ectoprocts (Figs. 28, 29): One short unisetose process present; process recumbent; calyx of setal socket produced into a tubular sheath which constricts base of modified seta; seta linear or slightly curved proximally, ventromedial surface shallowly impressed; base of process produced internally forming a short apodeme. Hemigonarcus (Fig. 30): Gonopleuron produced anteriorly beyond anterior margin of extrahemigonarcus; gonoplax absent; extrahemigonarcus an angular lobe anteriorly, narrowing posteriorly; hemigonarcal rib absent. Parameres (Figs. 31, 32): Apices of median lobes reflexed; lateral lobes absent; anterior lobes present, apices unexpanded; apophysis proxima narrow.

Remarks. Specimens of *Sympherobius arizonicus* cannot be confidently separated from dark specimens of *S. killingtoni* on the basis of forewing coloration. *Sympherobius arizonicus* and *S. killingtoni* are also the most difficult pair of species to separate on the basis of the male genitalia. In addition to the characters given in key couplet 31, the gonopleuron of *S. killingtoni* usually bears a small dark anterodorsal tooth (Fig. 25) which is absent in *S. arizonicus*.

I have examined specimens of *S. arizonicus* and/or *S. killingtoni* from northern Mexico which exhibit states of the ventromedial ectoproct process which are intermediate between the conditions normally found in these species.

Distributions and associations. Geographic distribution (Fig. 33): Arizona and California south to southern Mexico. Temporal distribution: January through December. Altitudinal distribution: 160′–5,350′ (49 m–1,631 m). Plant associations: no records.

Primary type material examined. Sympherobius arizonicus Banks. Holotype female. Verbatim label data: "Prescott / Arizona," "Collection / N. Banks," "Type / 11468," "Sympherobius / arizonicus / type Bks." Condition: fair, distal segments of hind legs, left forewing and pieces of other wings missing, otherwise complete.

Other material examined. 139 specimens. MEXICO: Baja California Norte, Baja California Sur, Oaxaca, Puebla and Sonora; UNITED STATES: Arizona, California. Institutions: ASUT, CAS, CU, LACM, MCZ, OSU, OSUC, PMY, TAMU, UAT, UCB, UCD, UCR, UMAA, UMSP, USNM.

<p align="center">*Sympherobius killingtoni* Carpenter
Figs. 6, 18–20, 23–27, 35</p>

Sympherobius killingtoni Carpenter, 1940:238 (OD, A, MG*, W*, Key). Holotype male. UNITED STATES: Utah: Juab Co., Eureka (MCZ type #23,675): Gurney, 1948 (MG*, Key); Nakahara, 1965a (Dst).
Sympherobius texanus Nakahara, 1965a:209 (OD, A, MG*, W*). Holotype male. UNITED STATES: Texas: Kerr Co., Kerrville (USNM). **New Synonym.**

Description. Antennae: Light to medium brown, usually darker basally and distally. Forewing (Figs. 18–20): Length 3.41–4.89 mm ($\bar{x}$ = 4.07, N = 25). Longitudinal veins hyaline to brown with distinct setal spotting; gradate crossveins brown and margined with brown; membrane pigmentation varies from mostly hyaline with scattered faint brown maculations to largely covered with brownish maculations divided by hyaline regions or spots; proximal and distal radial crossveins absent.

Male genitalia: Ectoprocts (Figs. 23, 24): One short unisetose process present; calyx
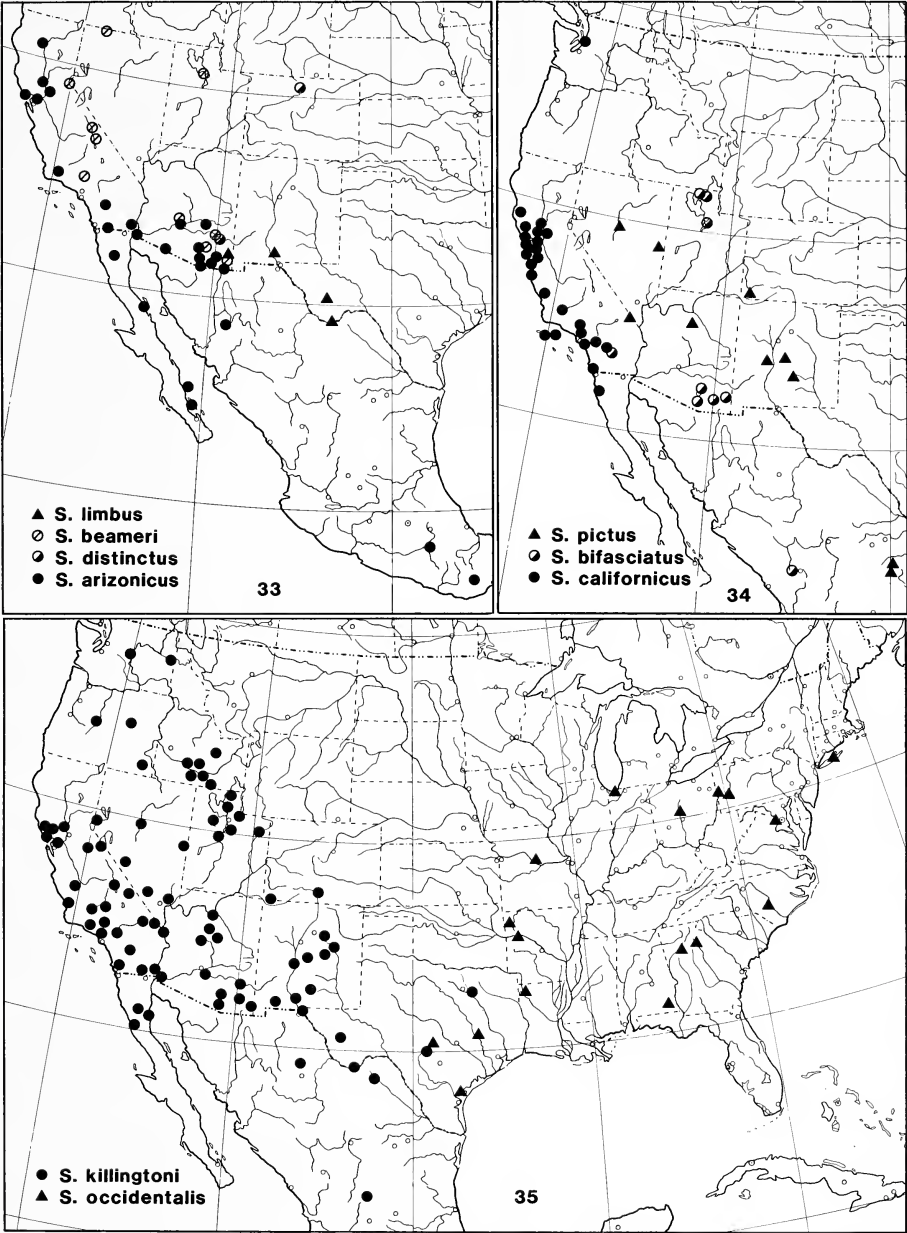
Figs. 33–35.   Geographic distributions of Nearctic *Sympherobius*. Only verified records plotted.

of setal socket produced into a tubular sheath loosely encircling base of modified seta; seta bent proximally, ventromedial surface impressed. Hemigonarcus (Fig. 25): Gonopleuron linear; anterior end nearly even with anterior margin of extrahemigonarcus; gonoplax absent or present as a small anterodorsal tooth; extrahemigonarcus a rounded lobe anteriorly, narrowed posteriorly; hemigonarcal rib absent. Parameres (Figs. 26, 27): Lateral lobes absent; anterior lobes present, apices unexpanded; apophysis proxima wide.

Remarks. Sympherobius texanus is a small specimen of *S. killingtoni.* Though the male genitalic structures of the holotype are slide mounted and therefore somewhat distorted, they are clearly identical to those of *S. killingtoni.*

The color and density of forewing maculations in *S. killingtoni* are quite variable. Darker specimens of *S. killingtoni* may be mistaken for *S. arizonicus.* Specimens with light or moderately dark maculations may resemble *S. perparvus* or *S. pictus* respectively. In *S. perparvus,* however, the forewing is narrower (Fig. 65), setal spotting is usually weak or absent and the forewing maculations usually consist of a number of relatively discrete spots or blotches set against a hyaline membrane. In *S. killingtoni* the wing is wider (Fig. 19), setal spotting is prominent and the membrane is usually lightly mottled with diffuse brown maculations. *Sympherobius pictus* also has prominent setal spotting but the discal maculations of the forewing are grouped into three or four irregular transverse bands (Fig. 22). See also *Remarks* under *S. arizonicus.*

Distributions and associations. Geographic distribution (Fig. 35): Western and south central United States and northern Mexico. Temporal distribution: January through December. Altitudinal distribution: 160'–10,150' (49 m–3,094 m). Plant associations: cypress.

Primary type material examined. Sympherobius killingtoni Carpenter. Holotype male. Verbatim label data: "Eureka / Ut. 13 - VII," "Spalding / Coll," "Collection / N. Banks," "23675 / M.C.Z. / Type," "Sympherobius / killingtoni Carp. / det. F. M. Carpenter." Condition: good, right foretarsus and left hindleg missing, otherwise complete. Genitalia in glycerin in microvial pinned below specimen.

Sympherobius texanus Nakahara. Holotype male. Verbatim label data: "Kerrville Tex / VI 1954 / L.J. Bottimer," "Holotype," "Sympherobius / texanus n. sp. / [Holotype] / W. Nakahara." Condition: Right forewing on one slide. Male genitalia on another slide. One leg, left forewing and right hindwing on point, remainder of body missing.

Other material examined. 324 specimens. MEXICO: Baja California Norte, Chihuahua, Coahuila, Zacatecas; UNITED STATES: Arizona, California, Colorado, Idaho, New Mexico, Nevada, Oregon, Texas, Utah, Washington. Institutions: AMNH, ASUT, CAS, CMP, CU, LACM, MCZ, OSU, OSUC, SMEK, TAMU, UAT, UCB, UCD, UCR, UMSP, USNM, WSU.

SYMPHEROBIUS PICTUS SPECIES GROUP

Sympherobius pictus (Banks)
Figs. 5, 22, 34, 36–39

Hemerobius pictus Banks, 1904c:62 (OD, A). Lectotype female. UNITED STATES: Colorado: "S.W.," precise locality unknown (MCZ type #11,488, designated by Carpenter, 1940, but see *Primary type material examined* below).
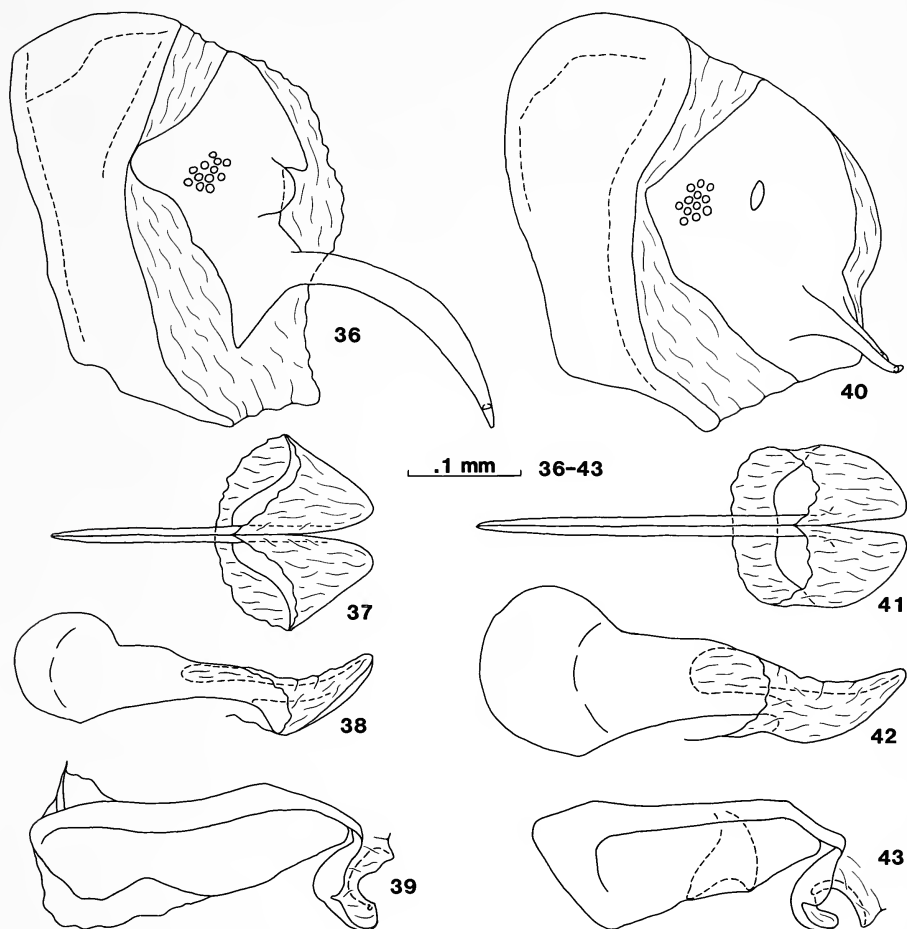
Figs. 36–43. *Sympherobius pictus*. 36. Ninth tergite and ectoproct, lateral. 37–38. Parameres, dorsal and lateral. 39. Gonarcus, lateral. *S. similis*. 40. Ninth tergite and ectoproct, lateral. 41–42. Parameres, dorsal and lateral. 43. Gonarcus, lateral.

Sympherobius pictus (Banks): Banks, 1905a (Tax); Banks, 1905b (RD, A, Dst, Key, Lst); Banks, 1907b (Lst); Banks, 1911 (Key); Carpenter, 1940 (RD, F, W*, Dst, Key).

Description. Antennae brown, concolorous. Legs: Male foretibia inflated (Fig. 5). Forewing (Fig. 22): Length 3.87–4.52 mm ($\bar{x}$ = 4.22, N = 6). Longitudinal veins largely hyaline; setal spotting prominent; most crossveins, including both gradate series, brown and widely margined with brown; tips of marginal veinlets dark brown; discal area dominated by three or four transverse brown bands; bands broad and irregular; apical and posterior wing margin also marked with a broad, irregular brown band broken at regular intervals by lighter colored regions; proximal and distal radial crossveins absent.
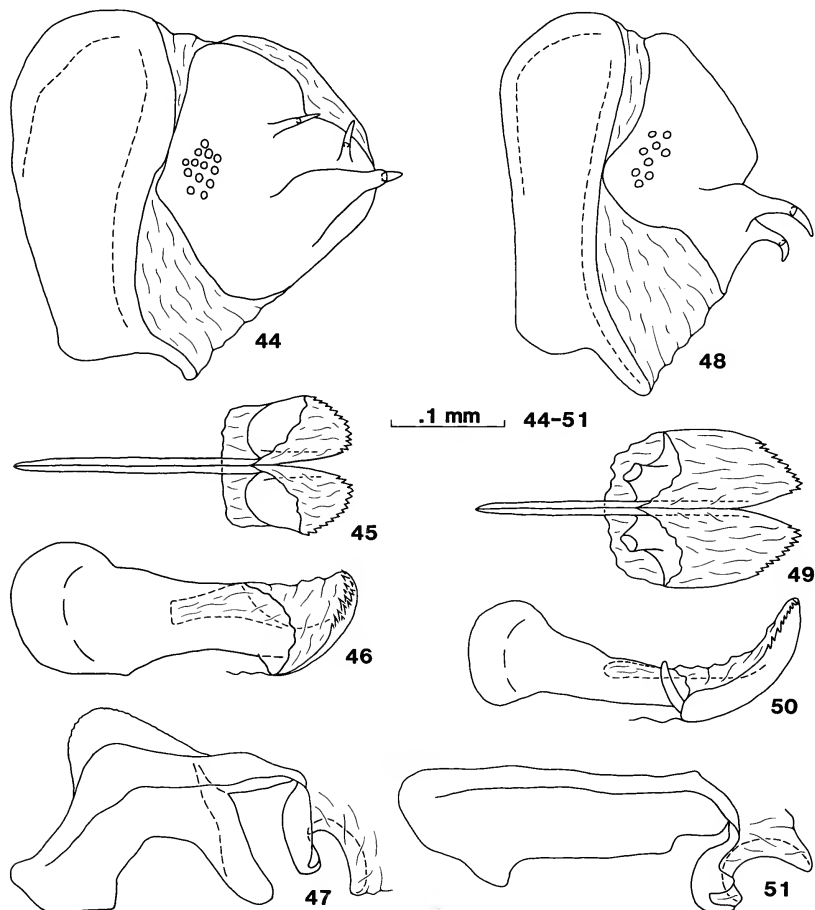
Figs. 44–51. *Sympherobius limbus*. 44. Ninth tergite and ectoproct, lateral. 45–46. Parameres, dorsal and lateral. 47. Gonarcus, lateral. *S. occidentalis.* 48. Ninth tergite and ectoproct, lateral. 49–50. Parameres, dorsal and lateral. 51. Gonarcus, lateral.

Male genitalia: Ectoprocts (Fig. 36): One very long unisetose process present; process directed ventrally with its greatest diameter near midlength, terminal seta very short; a broad setose tubercle present above base of ectoproct process. Hemigonarcus (Fig. 39): Gonopleuron linear or slightly sinuate, anterior end decurved; gonoplax a small triangular anterodorsal plate with a spiniform process; extrahemigonarcus moderately broad; hemigonarcal rib absent. Parameres (Figs. 37, 38): Anterolateral angle of median lobes forming an acute cusp in dorsal view; anterior and lateral lobes absent; apophysis proxima narrow.

Remarks. Males of *S. pictus* are unique in possessing an inflated foretibia (Fig. 5) and a single extremely long, unisetose ectoproct process (Fig. 36). Males and females may be distinguished from other species by the maculations of the discal area of the

forewing which are concentrated into three or four transverse bands (Fig. 22). See also *Remarks* under *S. killingtoni.*

Distributions and associations. Geographic distribution (Fig. 34): Southwestern United States and northern Mexico. Temporal distribution: 10 May through 15 August. Altitudinal distribution: 5,500'–7,200' (1,676 m–2,188 m). Plant associations: no records.

Primary type material examined. Sympherobius pictus Banks. Lectotype female. Verbatim label data: "S.W. Colo. / Oslar," "Collection / N. Banks," "TYPE / 11488," "Hemerobius / pictus / type Bks," "Lectotype / Sympherobius pictus / designated Carpenter / 1940 lectotype label / reapplied by Oswald 1985." Condition: left hindleg and right forewing missing, otherwise complete. One female paralectotype also seen, same data as lectotype (MCZ).

Carpenter (1940) examined the two female syntypes of *S. pictus* and stated "one of these has been now labelled the lectotype." Carpenter (1940:235, pl. 2, Fig. 13) figured the right forewing of the lectotype. I have reexamined the types and neither specimen now bears Carpenter's lectotype label. One syntype possesses both forewings, but the right forewing does not agree with Carpenter's figure. The second type is missing the right forewing (having been removed by Carpenter for figuring and now misplaced), but the left forewing agrees well with Carpenter's figure. This specimen is Carpenter's lectotype. To clarify the identity of this primary type I have applied the following label to the pin of this specimen: "Lectotype / Sympherobius pictus / designated Carpenter / 1940 lectotype label / reapplied by Oswald 1985."

Other material examined. 15 specimens. MEXICO: Nuevo Leon: 2 mi. N Pablillo, 2 specimens, 28.vii.1978 (TAMU); 2 mi. N La Ascension, 24.vii.1976 (TAMU); 23 mi. N La Escondida, 28.vii.1978 (TAMU). UNITED STATES: Arizona: Coconino Co.: 27 mi. NW Flagstaff on Rt. 180, 25.vi.1980, ex. *Pinus edulis* (AMNH). California: San Bernardino Co.: New York Mts., Live Oak Cyn., 25.v.1977 (UCR). Colorado: Montezuma Co.: Mesa Verde Nat. Park, 20.vi.1960 (USNM). New Mexico: Lincoln Co.: Ruidoso, 21.vi.1941 (UMSP). Socorro Co.: 12 mi. W Magdalena, 3 specimens, 15.viii.1982 (TAMU). Socorro or Torrance Co.: 2 mi. W Gran Quivera Nat. Mon., 10.v.1967 (USNM). Nevada: Lander Co.: Austin Summit, 2 specimens, 21.vii.1968 (UCB). White Pine Co.: Lehman Caves Nat. Mon., 14.viii.1963 (USNM).

Sympherobius similis Carpenter
Figs. 40–43, 66, 90

Sympherobius similis Carpenter, 1940:236 (OD, A, MG*, Key). Holotype male. UNITED STATES: Arizona: Santa Cruz or Pima Co., Santa Rita Mts. (SMEK).

Description. Forewing (Fig. 66): Length 3.80 mm (N = 1). Longitudinal veins brownish, anal veins hyaline; setal spotting absent; membrane hyaline with irregular light brown maculations; proximal radial crossvein present, distal radial crossvein absent.

Male genitalia: Ectoprocts (Fig. 40): Two unisetose processes present; processes adjacent and strongly incurved; each ectoproct of the only available male of this species contains a small oval hole in the ectoproct near the calus cercus, these openings are located in approximately the position a dorsolateral process would originate and may be remnants of a third broken ectoproct process. Hemigonarcus (Fig. 47): An-

terior end of gonopleuron decurved; gonoplax absent or narrow and elongate; extra-hemigonarcus moderately broad; hemigonarcal rib present, forked. Parameres (Figs. 45, 46): Median lobes weakly tanned, their margins indistinctly delimited; anterior and lateral lobes absent; apophysis proxima moderately broad.

Remarks. The forewing maculations of *S. similis* are similar to those of *S. bifasciatus, S. constrictus* and *S. quadricuspis* but with the longitudinal veins nearly evenly brown, not with distinct alternating dark and hyaline segments. The shape of the parameres and forked hemigonarcal ribs of the extrahemigonarcus will also distinguish this species.

Distributions and associations. Geographic distribution (Fig. 90): Known only from the Santa Rita Mountains of southern Arizona. Temporal distribution: 20 June and 17 July. Altitudinal distribution: no records. Plant associations: no records.

Primary type material examined. Sympherobius similis Carpenter. Holotype male. Verbatim label data: "Santa Rita Mts / Ar. 7-17-32 / R. H. Beamer," "Type," "Sympherobius / similis Carp. / Holotype." Condition: good, right mesotibia and tarsus, pedicle and flagellum of left antenna and distal portion of right antenna missing, otherwise complete. Left forewing slide mounted in Hoyer's solution. Genitalia in glycerin in microvial pinned below specimen. Ninth sternite missing.

Other material examined. 1 specimen. UNITED STATES: Arizona: Santa Cruz or Pima Co.: Santa Rita Mts., 20.vi.[year unrecorded] (USNM).

Sympherobius occidentalis (Fitch)
Figs. 35, 48–51, 63

Hemerobius occidentalis Fitch, [1855] 1854:799 (OD, A). Syntype(s?), sex(s) unknown. UNITED STATES: Illinois: Henderson River, precise locality unknown. Type material apparently lost, see under *Types* below.: Banks, 1892 (Lst).

Sympherobius occidentalis (Fitch): Banks, 1905b (RD, A, Dst, Key, Lst); Banks, 1907b (Lst); Banks, 1911 (Key); Smith, 1934 (Dst, Key); Brimley, 1938 (Dst); Carpenter, 1940 (RD, A, MG*, W*, Dst, Key, Tax); Froeschner, 1947 (Dst); Throne, 1971 (Dst); Agnew et al., 1981 (A*, Dst, Key).

Spadobius occidentalis (Fitch): not Needham, 1905 (see *S. amiculus*); Krüger, 1922 (Tax).

Description. Antennae: Anterior face of scape and pedicle yellow, posterior face brownish; proximal segments of flagellum dark brown, distal segments yellow to yellow-brown. Mesonotum: Brown with an anteriorly opening yellow "V" formed by yellow markings on the prescutum, scutum and scutellum; prescutum also bisected by a longitudinal yellow stripe. Forewing (Fig. 63): Length 3.80–5.23 mm ($\bar{x}$ = 4.32, N = 25). Longitudinal veins and crossveins monochromatic dark brown, except yellowish base of radius; veins narrowly margined with brown, particularly crossveins and veins of cubital and anal regions; cells with brownish centers surrounded by hyaline membrane; brownish centers of cells in discal area with light brown to hyaline median stripes, proximal radial crossvein present, distal radial crossvein absent.

Male genitalia: Ectoprocts (Fig. 48): Two unisetose processes present; processes short, heavily tanned and decurved. Hemigonarcus (Fig. 51): Gonopleuron linear or slightly decurved anteriorly; gonoplax absent; extrahemigonarcus moderately broad; hemigonarcal rib absent. Parameres (Figs. 49, 50): Apices of medial lobes angulate,

margins armed with large teeth; lateral lobes absent; anterior lobes present, apices unexpanded; apophysis proxima narrow.

Remarks. The largely brown to fuscous forewing cells of *S. occidentalis* are similar to those of *S. umbratus* but the male genitalia of *S. occidentalis* possess only two ectoproct processes and the lateral lobes of the parameres are absent. *Sympherobius occidentalis* is also unique in possessing a prominent yellow or pale V-shaped mark on the mesonotum.

Distributions and associations. Geographic distribution (Fig. 35): Eastern United States. Temporal distribution: 20 April through 25 October. Altitudinal distribution: no records. Plant associations: *Pinus* sp.

Types. Carpenter (1940:231) stated that Fitch's type material of *S. occidentalis* was not in the MCZ or USNM, and was apparently lost. Lacking specimens of the species he treated as *S. occidentalis* from the type locality (Illinois) of *S. occidentalis* Fitch, Carpenter refrained from designating a neotype for this species.

Of the 17 Nearctic species of *Sympherobius* two, *S. umbratus* (=Carpenter's *S. gracilis* + *S. umbratus*) and *S. occidentalis,* possess the lack of mottling and "two faint parallel lines of a more dusky tinge" mentioned by Fitch ([1855] 1854:799) as characteristic of the discal cells of the forewing of *S. occidentalis.* However, *S. occidentalis* is distinguishable from *S. umbratus* on the basis of Fitch's original description of the forewing venation of *S. occidentalis*: "outer fork of the first discoidal vein [=R4+5] anastamosing [i.e., joined by a crossvein] with the rib-vein [=radial stem] near its base instead of with the second discoidal [=R2+3] as in the preceding species [i.e., *S. amiculus*]." In *S. occidentalis* the proximal radial crossvein joins the R4+5 ["outer fork of first discoidal"] to the R1+2+3 ["rib-vein"], as described by Fitch; in *S. amiculus* and *S. umbratus* the distal radial crossvein joins the R4+5 ["outer fork of first discoidal"] to the R2+3 ["second discoidal"]. Since the identity of *S. occidentalis* is not in question, designation of a neotype is unwarranted (ICZN, 1985: Article 75). The species treated here as *S. occidentalis* is the same as that treated by Carpenter under the same name.

Material examined. 43 specimens. UNITED STATES: Alabama, Arkansas, Georgia, Louisiana, Missouri, North Carolina, New York, Ohio, Pennsylvania, Texas, Virginia. Institutions: AMNH, CMP, CU, FEM, INHS, LSU, NCSR, OSU, SMEK, TAMU, UCB, UGA, UMC, USNM. Also recorded from UNITED STATES: District of Columbia, Kansas, Wisconsin (Carpenter, 1940—District of Columbia; Banks, 1905b—Kansas; Throne, 1971—Wisconsin).

Sympherobius limbus Carpenter
Figs. 21, 33, 44–47

Sympherobius limbus Carpenter, 1940:236 (OD, A, MG*, Key). Holotype male. UNITED STATES: Texas: Brewster Co., Alpine (SMEK).

Description. Antennae: Flagellum brown, concolorous. Forewing (Fig. 21): Length 3.80–4.24 mm ($\bar{x}$ = 4.04, N = 3). Longitudinal veins brownish yellow, concolorous or with alternating lighter brown segments; setal spotting weak; membrane hyaline or mottled with diffuse light brown maculations; vein setae pale; crossveins diffusely margined with light brown; proximal and distal radial crossveins absent.

Male genitalia: Ectoprocts (Fig. 44): Three unisetose processes present; ventral

processes incurved; ventrolateral process very stout, lateral surface with several normal setae in addition to terminal modified seta; dorsolateral process short. Hemigonarcus (Fig. 47): Anterior end of gonopleuron angled ventrally; gonoplax a prominent curved plate; ventral margin of extrahemigonarcus broadly emarginate; hemigonarcal rib present, unforked. Parameres (Figs. 45, 46): Posterior margins toothed; anterior and lateral lobes absent; apophysis proxima broad.

Remarks. Sympherobius limbus may be distinguished from other species without proximal or distal radial crossveins by its faint setal spotting and diffuse yellowish brown membrane. Its male genitalia resemble *S. similis* in lacking both anterior and lateral lobes of the parameres and in possessing the hemigonarcal rib of the extrahemigonarcus, but in *S. similis* the median lobes of the parameres are without teeth and the hemigonarcal ribs are forked.

Distributions and associations. Geographic distribution (Fig. 33): Southwestern United States. Temporal distribution: June through 4 October. Altitudinal distribution: 5,400′–7,600′ (1,646 m–2,316 m). Plant associations: no records.

Primary type material examined. Sympherobius limbus Carpenter. Holotype male. Verbatim label data: "Alpine, Texas / 7-11-28 / R. H. Beamer," "Type," "Sympherobius / limbus Carp. / Holotype." Condition: good, tips of antennae and several small pieces of wings missing, otherwise complete. Genitalia in glycerin in microvial pinned below specimen.

Other material examined. 4 specimens. UNITED STATES: Arizona: Cochise Co.: Chiricahua Mts., Onion Saddle, 25.vii.1966 (CU); S.W. Research Station, 5 mi. S Portal, vi.1967 (USNM). New Mexico: Dona Ana Co.: Aguirre Sprs. 5 mi. S San Augustine Pass, 23.viii.1971 (UCD). Texas: Brewster Co.: The Basin, Big Bend Nat. Park, 4.x.1956 (UCB).

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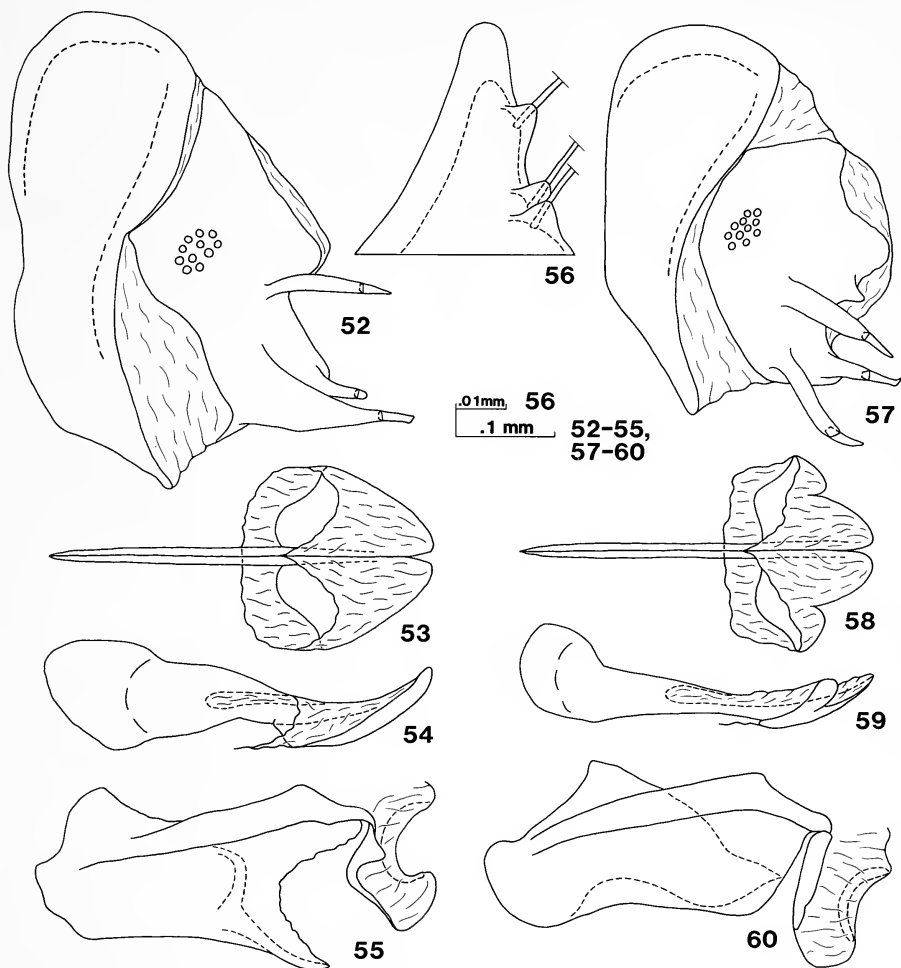*Sympherobius distinctus* Carpenter
Figs. 33, 52–55, 61

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Sympherobius distinctus Carpenter, 1940:238 (OD, A, MG*, Key). Holotype male. UNITED STATES: Colorado: Larimer Co., Pingree Park (MCZ type #23,677).

Description. Antennae dark brown, concolorous. Forewing (Fig. 61): Length 6.76 mm (N = 1). Longitudinal veins evenly brown, not interrupted by hyaline segments; setal spotting absent; gradate crossveins brown; membrane light brown with irregular hyaline spots or blotches; posterior costal margin with several hyaline regions; proximal and distal radial crossveins absent.

Male genitalia: Ectoprocts (Fig. 52): Three unisetose processes present; dorsolateral process straight; ventral processes incurved. Hemigonarcus (Fig. 55): Gonopleuron linear; gonoplax a broad rounded lobe; extrahemigonarcus moderately broad; hemigonarcal rib present, produced posteroventrally into a narrow elongate process. Parameres (Figs. 53, 54): Median lobes not toothed; lateral and anterior lobes absent; apophysis proxima moderately broad.

Remarks. Sympherobius distinctus is the largest Nearctic *Sympherobius* species. The brownish longitudinal radial veins and membrane of the forewing are similar to those of *S. umbratus,* but the membrane of *S. distinctus* is marked with irregular hyaline regions. The proximal and distal radial crossveins are also absent in *S. distinctus.* The male parameres are similar to those of *S. pictus, S. limbus* and *S.*

Figs. 52–60. *Sympherobius distinctus.* 52. Ninth tergite and ectoproct, lateral. 53–54. Parameres, dorsal and lateral. 55. Gonarcus, lateral. *S. angustus.* 56. Enlargement of dorsomedial prominence. 57. Ninth tergite and ectoproct, lateral. 58–59. Parameres, dorsal and lateral. 60. Gonarcus, lateral.

similis in lacking both the anterior and lateral lobes, but *S. distinctus* is distinguished by the elongate hemigonarcal rib.

Distributions and associations. Geographic distribution (Fig. 33): Known only from Arizona and Colorado at high elevation. Temporal distribution: 18 and 19 August. Altitudinal distributions: 9,050′ (2,758 m). Plant associations: no records.

Primary type material examined. Sympherobius distinctus Banks. Holotype male. Verbatim label data: "Pingree Park Colo / Aug 18 1926," "RCSmith / Collector," "M.C.Z. / Type / 23677," "Sympherobius / distincta Carp. / det. F.M. Carpenter." Condition: fair, right foreleg distal to femur and antennae distal to scapes absent.

Tip of right forewing also missing, otherwise complete. Left forewing slide mounted in Hoyer's solution. Genitalia in glycerin in microvial pinned below specimen.

Other material examined. 1 specimen. UNITED STATES: Arizona: Graham Co.: Graham Mts., Hospital Flat, 19.viii.1952 (USNM).

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SYMPHEROBIUS ANGUSTUS SPECIES COMPLEX

Sympherobius angustus (Banks)
Figs. 4, 56–60, 76–78, 90

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Hemerobius angustus Banks, 1904a:102 (OD, A). Lectotype female. UNITED STATES: New Mexico: Dona Ana Co., Mesilla (MCZ type #11,485, designated by Carpenter, 1940).

Sympherobius angustus (Banks): Banks, 1905a (Dst); Banks, 1905b (RD, A, MG*, Dst, Key, Lst); Banks, 1907b (Lst); not Essig, 1910 (see *S. californicus*); Banks, 1911 (Key); Cole, 1933 (Bic, Bio, Par); Carpenter, 1940 (RD, F, W*, Dst, Key); Spencer, 1942 (Dst); Nakahara, 1965a (Dst); Nakahara, 1965b (Dst).

Sympherobius tristis Navás, 1914a:15 (OD, A, W*). Holotype, sex unknown. UNITED STATES: New Mexico: San Miguel Co., Pecos (not examined, repository unknown): Carpenter, 1940 (Tax).

*Nefasitus tristis* (Navás): Navás, 1915c (Tax).

Sympherobius stangei Nakahara, 1960:16 (OD, A, W*). Holotype, sex unknown. UNITED STATES: California: San Bernardino Co., Barton Flats (not examined, repository unknown, probably in Nakahara Collection, Japan [Lionel Stange, pers. comm.]): Nakahara, 1965a (Dst). **New Synonym.**

Sympherobius brunneus Nakahara, 1965a:207 (OD, A, MG*, W*). Holotype male. UNITED STATES: California: Mariposa Co., Miami Ranger Station (CAS Entomology Type #9062): Flint, 1966 (Tax). **New Synonym.**

Description. Antennae: flagellum brown, monochromatic. Forewing (Figs. 77–79): Length 4.78–6.36 mm ($\bar{x} = 5.50$, N = 25). Pigmentation pattern of longitudinal veins variable, typically with alternating brown or fuscous and hyaline segments, in some specimens (*stangei* color form) proximal regions of longitudinal veins entirely fuscous with hyaline segments present only distally on some radial veins; veins unmargined to widely margined with fuscous; setal spotting absent; membrane largely hyaline (*stangei* color form), diffusely mottled (typical color form) or evenly tinged with light brown (*brunneus* color form); Cu1 distal to Cu1–Cu2 fork frequently broadly margined with fuscous; gradate crossveins brown to fuscous usually margined with fuscous; proximal radial crossvein present (rarely absent or double), distal radial crossvein absent.

Male Genitalia: Ectoprocts (Figs. 56, 57): Three unisetose processes and dorsomedial prominence present; ventral and dorsolateral processes incurved, ventrolateral process most strongly curved. Hemigonarcus (Fig. 60): Gonopleuron linear; gonoplax variable, large and triangular (as figured) or low and broadly rounded dorsally; extrahemigonarcus broad; hemigonarcal rib present, unforked. Parameres (Figs. 58, 59): Lateral lobes broad (rarely narrowed), posterior margin curved dorsally; anterior lobes absent; apophysis proxima narrow.

Remarks. Nakahara described *S. brunneus* on the basis of the immaculate light
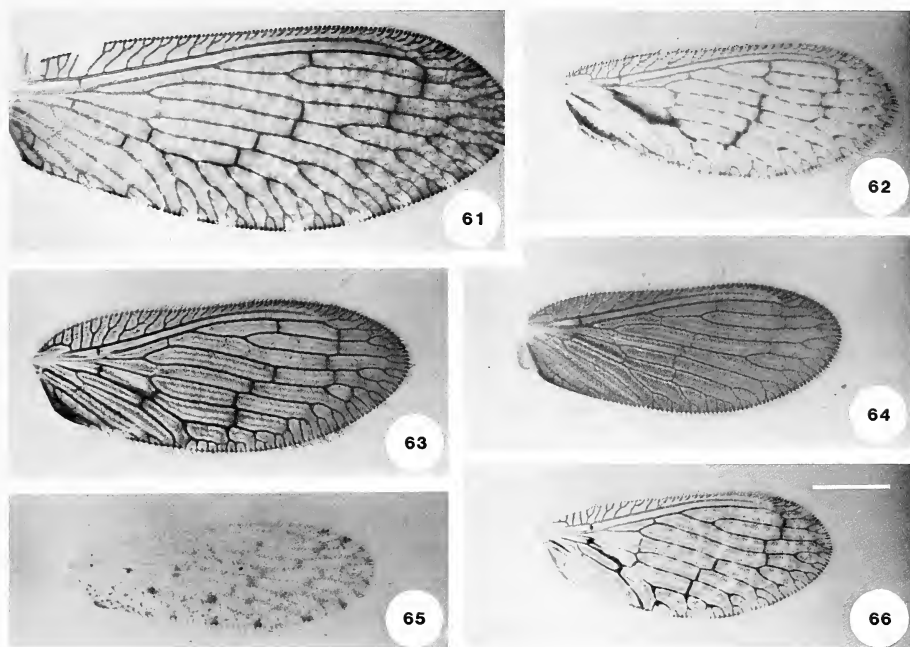
Figs. 61–66. Forewings of *Sympherobius*. 61. *S. distinctus*. 62. *S. quadricuspis*. 63. *S. occidentalis*. 64. *S. umbratus*. 65. *S. perparvus*. 66. *S. limbus*. Scale bar = 1 mm. All figures to same scale.

brown tinting of the forewing membrane and *S. stangei* primarily on the basis of the broad fuscous margining of the longitudinal veins of the forewing. Although these forms are distinct phenotypes based on forewing coloration, the male genitalia of both forms are indistinguishable from those of *S. angustus* and I consider them junior synonyms.

Sympherobius brunneus appears to be a color form of *S. angustus* endemic to the Sierra Nevada and Siskiyou mountains of northern California. I have seen specimens of this color form only from four counties in northern California: Mariposa (1 specimen), Placer (1), Siskiyou (7) and Tuolumne (1). The *brunneus* color form (Fig. 77) is sympatric with the typical *angustus* color form (Fig. 78) in the Sierra Nevada mountains (typical color form seen from El Dorado, Nevada, Placer and Tuolumne counties). I have not seen the typical *angustus* color form from the Siskiyou mountains.

The type of *S. stangei* was described from material sent to the late Dr. Waro Nakahara in Japan by Dr. Lionel Stange. The type of this species has not been examined. However, since the abdomen of the type is missing, its usefulness in verifying the presently proposed synonymy of *S. stangei* and *S. angustus* would be limited. Several male specimens (from California: El Dorado Co., San Diego Co.; Colorado: Chimney Gulch; and Oregon: Harny Co.) with the same extensive fuscous margining of the forewing veins (Fig. 76) shown by Nakahara's figure of the forewing
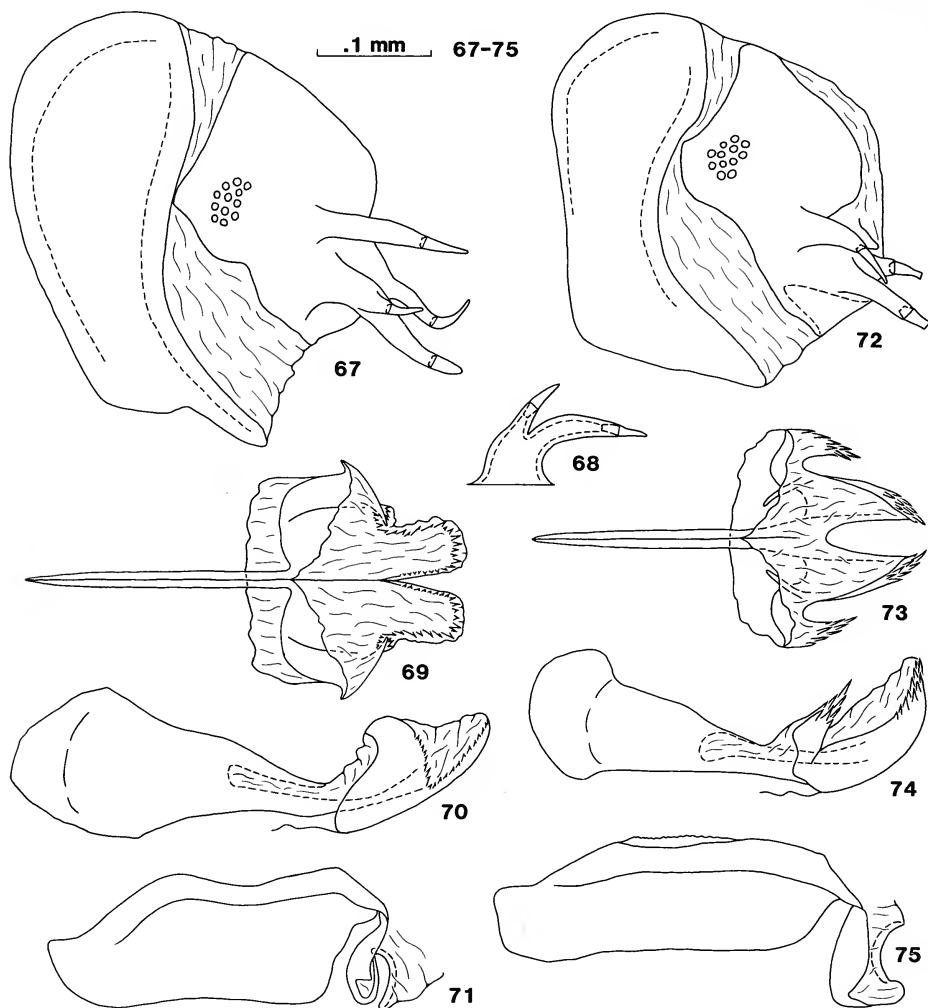
Figs. 67–75. *Sympherobius bifasciatus.* 67. Ninth tergite and ectoproct, lateral. 68. Ventro-lateral ectoproct process. 69–70. Parameres, dorsal and lateral. 71. Gonarcus, lateral. *S. quad-ricuspis.* 72. Ninth tergite and ectoproct, lateral. 73–74. Parameres, dorsal and lateral. 75. Gonarcus, lateral.

of the holotype of *S. stangei* (Nakahara, 1960, Fig. 13) have been examined. On the basis of male genitalic characters, these specimens are indistinguishable from *S. angustus.*

As indicated above *S. angustus* is extremely variable in forewing pigmentation. Typical *angustus* color forms are easily confused with *S. californicus, S. constrictus, S. bifasciatus* and *S. quadricuspis.* In each of these five species the proximal radial crossvein is present, the distal radial crossvein is absent and the longitudinal veins

are normally marked with alternating brown and hyaline segments. *Sympherobius californicus* may usually be distinguished by the absence of the elongate dark maculation along the Cu1, and the light brown to yellowish central region of the antennal flagellum. *Sympherobius bifasciatus* may be distinguished by the hyaline or only spotted basal third of the 1A. Specimens exhibiting extensive fuscous margining of the longitudinal R, M and Cu veins (Fig. 76) may be confidently referred to *S. angustus*.

Because of limited material, the full range of variation in the forewing maculation patterns of *S. constrictus* and *S. quadricuspis* is unknown, with the known variation overlapping that of *S. angustus*. Consequently, confident identification of these species cannot be obtained without examination of the male genitalia.

Although *S. angustus, S. californicus, S. constrictus, S. bifasciatus* and *S. quadricuspis* are difficult to separate with forewing characters, the male genitalia, particularly the shape of the median and lateral lobes of the parameres, are very distinctive for each species.

Distributions and associations. Geographic distribution (Fig. 90): *Sympherobius angustus* is a montane species restricted to middle and high elevations of southwestern Canada, the western United States and Mexico. Temporal distribution: 25 May through 8 October. Altitudinal distribution: 3,600′–9,600′ (1,097 m–2,926 m). Plant associations: *Picea* sp. Prey records: *Pseudococcus citri* (see Cole, 1933).

Primary type material examined. Hemerobius angustus Banks. Lectotype female. Verbatim label data: "type," "Type / 11485," "Collection / N. Banks," "Mesilla / NM," "Hemerobius / angustus / type Bks," "Lectotype." Condition: good, tips of antennae and some tarsal segments missing, otherwise complete.

Sympherobius brunneus Nakahara. Holotype male. Verbatim label data: "Miami Ranger Sta / Mariposa Co. Cal.," "H.P. Chandler / No. 21 Expo. / 7/5/45 NE / Elv. 5,000 SW," "H. Chandler / Collection," "Sympherobius / brunneus n. sp. / [Holotype] / W. Nakahara," "Holotype." Condition: poor, left forewing on one slide, male genitalia on another slide, parts of right forewing, right eye and one leg on point, remainder of specimen missing.

Other material examined. 88 specimens. CANADA: British Columbia; MEXICO: Durango, Mexico, Nuevo Leon, Oaxaca; UNITED STATES: Arizona, California, Colorado, Idaho, New Mexico, Nevada, Oregon, South Dakota, Utah. Institutions: CAS, CSU, CU, LACM, MCZ, OSU, OSUC, SMEK, TAMU, UAT, UCB, UCD, UCR, UNH, USNM. Also recorded from MEXICO: Morelos (Nakahara, 1965b). Nakahara's 1965b records from Mexico: Veracruz and Jalapa are not *S. angustus*.

Sympherobius quadricuspis, new species
Figs. 62, 72–75, 113

Description. Antennae: Light brown. Forewing (Fig. 62): Length 4.32 mm (N = 1). Longitudinal veins light brown interrupted by hyaline segments; membrane hyaline or very faintly mottled; gradate crossveins brown and margined with brown; central region of Cu1, basal portion of 1A and 3A and posterior fork of 2A margined with brown; proximal radial crossvein present, distal radial crossvein absent.

Male genitalia: Ectoprocts (Fig. 72): Three unisetose processes and dorsomedial prominence present; ventral processes incurved. Hemigonarcus (Fig. 75): Gonopleu-
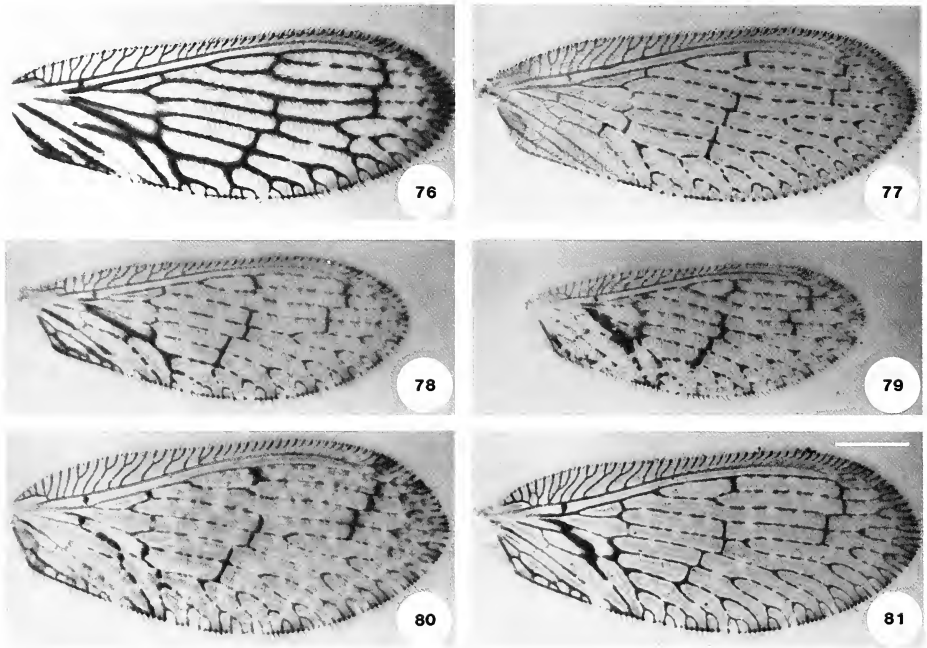
Figs. 76–81. Forewings of *Sympherobius*. 76. *S. angustus, stangei* color form. 77. *S. angustus, brunneus* color form. 78. *S. angustus,* typical color form. 79. *S. bifasciatus.* 80. *S. californicus.* 81. *S. constrictus.* Scale bar = 1 mm. All figures to same scale.

ron linear; gonoplax narrow and elongate; extrahemigonarcus moderately broad, produced anteriorly beyond end of gonopleuron; hemigonarcal rib absent. Parameres (Figs. 73, 74): Apices of median and lateral lobes acutely angled, armed with very large teeth; median lobes divided by a deep U-shaped emargination; lateral lobes narrow; anterior lobes present; apophysis proxima narrow.

Etymology. From the Greek "quadri-," four, and "cuspis," point, in reference to the acute apices of the median and lateral lobes of the parameres.

Remarks. For a discussion of similar species see *Remarks* under *S. angustus.*

Distributions and associations. Geographic distribution (Fig. 113): Known only from the Chiricahua Mountains of southeastern Arizona. Temporal distribution: 30 April and 25 July. Altitudinal distribution: 5,400'–7,600' (1,646 m–2,316 m). Plant associations: no records.

Primary type material examined. Sympherobius quadricuspis, n. sp. Holotype male. UNITED STATES: Arizona: Cochise Co.: Southwestern Research Station, 5 mi. W Portal (AMNH). Verbatim label data: "S.W.R.S., 5 mi. W. / Portal Cochise / Co., ARIZ. 5400 ft. / IV-22-30-1963," "Vincent Roth / Collector," "Holotype / Sympherobius / quadricuspis Oswald." Condition: good, antennae distal to scapes missing. Genitalia in glycerin in microvial pinned below specimen.

Other material examined. One male paratype. UNITED STATES: Arizona: Cochise Co.: Chiricahua Mts., Onion Saddle, 25.vii.1966 (CU).

Sympherobius bifasciatus Banks
Figs. 34, 67–71, 79

Sympherobius bifasciatus Banks, 1911:347 (OD, A, Key). Holotype male. UNITED
  STATES: Colorado: precise locality unknown (MCZ type #11,490): Carpenter,
  1940 (RD, A, MG*, Dst, Key); Nakahara, 1965a (Dst).

Description. Scape and pedicle dark brown. Flagellum yellow-brown proximally
and distally, yellow medially. Forewing (Fig. 79): Length 4.06–4.94 mm ($\bar{x}$ = 4.48,
N = 3). Longitudinal veins brown with irregularly spaced hyaline segments; hyaline
segments without setal spotting; membrane hyaline or faintly mottled with light
brown; most crossveins and distal forks of longitudinal veins margined with brown;
membrane adjacent to central region of Cu1 forming a brown macula; proximal
radial crossvein present, distal radial crossvein absent.
  Male genitalia: Ectoprocts (Figs. 67, 68): Three processes present; dorsolateral and
ventromedial processes unisetose; ventrolateral process bisetose; ventrolateral pro-
cess deeply forked, base wide. Hemigonarcus (Fig. 71): Gonopleuron with anterior
end directed ventrally; gonoplax absent or narrow and elongate; extrahemigonarcus
broad; hemigonarcal rib absent. Parameres (Figs. 69, 70): Apical margin of median
lobes squarish, armed with very large teeth; lateral lobes curved dorsally; anterior
lobes absent; apophysis proxima narrow.
  Remarks. For a discussion of similar species see *Remarks* under *S. angustus.*
  Distributions and associations. Geographic distribution (Fig. 34): Southwestern
United States and northern Mexico. Temporal distribution: 12 June through 20
October. Altitudinal distribution: 5,400′–8,400′ (1,646 m–2,560 m). Plant associa-
tions: Pine-Oak zone (southern Arizona).
  Primary type material examined. Sympherobius bifasciatus Banks. Holotype male.
Verbatim label data: "Colo / 1527," "Collection / N. Banks," "Type / 11490,"
"Sympherobius / bifasciatus / type Bks." Condition: good, antennae distal to scapes
absent, apex of right forewing missing, otherwise complete. Genitalia in glycerin in
microvial pinned below specimen. Ninth sternite and parameres missing.
  Other material examined. 46 specimens. MEXICO: Durango; UNITED STATES:
Arizona, California, Colorado, Utah. Institutions: CU, MCZ, OSU, UAT, UCB,
UCR, UMSP, USNM. Also recorded from CANADA: Alberta (Carpenter, 1940).

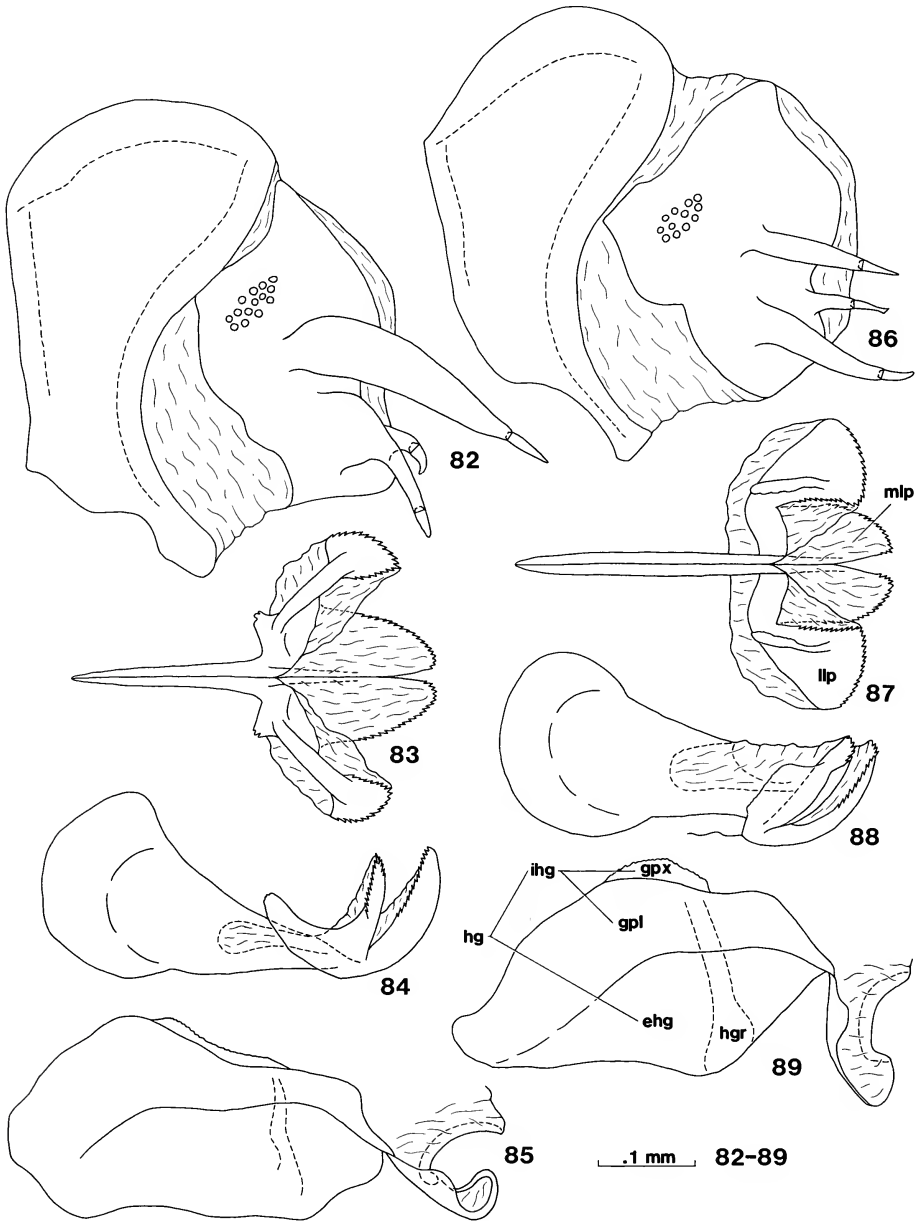*Sympherobius californicus* Banks
Figs. 34, 80, 86–89

Hemerobius californicus Banks, 1905a:90. Nom. Nud. (see *Remarks* below).
[*Sympherobius angustus* (Banks): Essig, 1910 (A*, P*, PP*, L*, Bic, Bio). Misiden-
  tification.]
Sympherobius californicus Banks, 1911:346 (OD, A, MG*, Key). Lectotype male.
  UNITED STATES: California: Los Angeles Co., Pasadena (MCZ type #11,487,
  designated by Carpenter, 1940): Cole, 1933 (Bic, Bio, Par); Carpenter, 1940 (RD,
  A, MG*, W*, Dst, Key); Nakahara, 1960 (Dst, Tax); Nakahara, 1965a (Dst).
Nefasitus californicus (Banks): Navás, 1915c (Tax).

Description. Antennae: Flagellum usually brownish proximally and distally, sep-
arated by a lighter yellowish or light brown region. Forewing (Fig. 80): Length 4.41–

Figs. 82–89. *Sympherobius constrictus.* 82. Ninth tergite and ectoproct, lateral. 83–84. Parameres, dorsal and lateral. 85. Gonarcus, lateral. *S. californicus.* 86. Ninth tergite and ectoproct, lateral. 87–88. Parameres, dorsal and lateral. 89. Gonarcus, lateral. Abbreviations: ehg, extrahemigonarcus; gpl, gonopleuron; gpx, gonoplax; hg, hemigonarcus; hgr, hemigonarcal rib; ihg, intrahemigonarcus; llp, lateral lobe of parameres; mlp, median lobe of parameres.

6.47 mm ($\bar{x}$ = 5.62, N = 25). Longitudinal veins with brown and hyaline segments of irregular length; setal spotting absent; membrane mottled with irregular brown maculations; crossveins dark brown and margined with brown; proximal radial crossvein present (rarely absent), distal radial crossvein absent.

Male genitalia: Ectoprocts (Fig. 86): Three unisetose processes present; ventral processes incurved, ventrolateral process strongly curved; dorsolateral process straight. Hemigonarcus (Fig. 89): Gonopleuron broad, angled ventrally near midlength; gonoplax narrow and elongate; extrahemigonarcus broad; hemigonarcal rib present, unforked. Parameres (Figs. 87, 88): Apices of median lobes angulate, margins armed with large teeth; lateral lobes subtriangular, attached narrowly to anterolateral corner of median lobes, apical margins with large teeth; lateral lobes with an erect longitudinal keel on the dorsal surface; anterior lobes absent; apophysis proxima broad.

Remarks. The name *Hemerobius californicus* Banks was published without description or indication and is thus a nomen nudum. Based on the facts that the specimens listed as *H. californicus* were collected near Stanford University (Palo Alto, California), a locality well within the range of *S. californicus,* and that no other hemerobiid shares the specific name '*californicus,*' it seems probable that the material listed under this name was specimens of *S. californicus.*

Essig's (1910) figure of "*Sympherobius angustus*" and his statement that adults were still emerging in January clearly indicate that the species he studied was *S. californicus,* not *S. angustus.* Temporal records from pinned specimens indicate that *S. californicus* adults are commonly present throughout the winter months in California while adults of *S. angustus,* a montane species, are not.

For a discussion of similar species see *Remarks* under *S. angustus.*

Distributions and associations. Geographic distribution (Fig. 34): *Sympherobius californicus* is a lowland species common to extreme northwestern Mexico and western California. One male from Seattle, Washington, has also been examined. This species is absent from the montane regions of northern and eastern California and the Mohave Desert of southeastern California. Temporal distribution: January through December. Altitudinal distribution: 250'–840' (76 m–256 m). Plant associations: Orange.

Primary type material examined. Sympherobius californicus Banks. Lectotype male. Verbatim label data: "type," "Mark [?] F.Grinnell, Jr / Los Angeles County / Pasadena Calif.," "Collection / N. Banks," "Type / 11487," "Sympherobius / californicus / type Bks." Condition: good, right hindleg, left metatarsus and distal segments of antennae missing, otherwise complete. Genitalia in glycerin in microvial pinned below specimen.

Other material examined. 446 specimens. MEXICO: Baja California Norte; UNITED STATES: California, Washington. Institutions: ASUT, CAS, CU, LACM, MCZ, OSUC, SMEK, UCB, UCD, UCR, USNM.

Sympherobius constrictus, new species
Figs. 81–85, 90

Description. Flagellum brownish, central region lighter brown. Forewing (Fig. 81): Length 4.84–6.43 mm ($\bar{x}$ = 5.63, N = 6). Longitudinal veins light brown interrupted by short hyaline segments; setal spotting absent; vein setae pale and inconspicuous
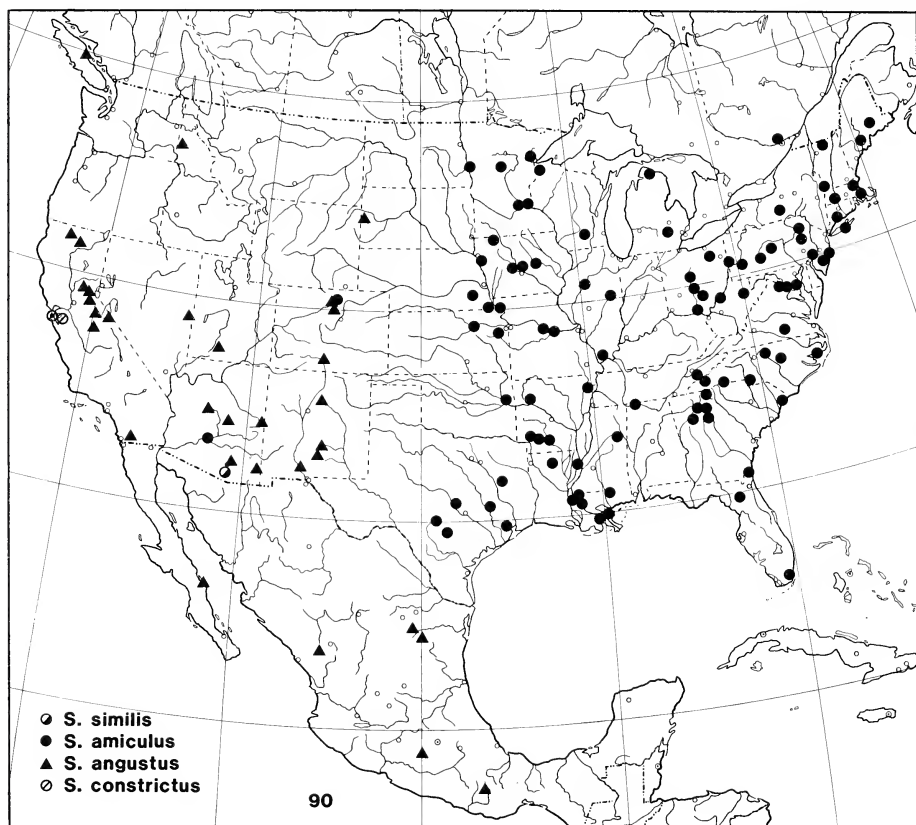
Fig. 90.   Geographic distributions of Nearctic *Sympherobius*. Only verified records plotted.

against membrane; Cu1 distal to Cu1-Cu2 fork with an elongate brown maculation; crossveins brown and margined with brown; membrane hyaline, except for brown margining of some veins; proximal radial crossvein present, distal radial crossvein absent.

Male genitalia: Ectoprocts (Fig. 82): Three unisetose processes present; ventromedial and ventrolateral processes curved ventromedially; dorsolateral process straight, constricted at base. Hemigonarcus (Fig. 85): Gonopleuron widened anteriorly; gonoplax narrow and elongate; extrahemigonarcus broad; hemigonarcal rib present, unforked. Parameres (Figs. 83, 84): Median lobes rounded apically, margins with large teeth; lateral lobes small subtriangular plates supported by narrow sclerotized rods arising from anterolateral region of median lobes, margins with large teeth; anterolateral corners of median lobes elongate; apophysis proxima narrow.

Etymology. From the Latin "constrictus," drawn together or contracted, in reference to the constricted base of the dorsolateral ectoproct spine.

Remarks. Sympherobius constrictus is closely related to *S. californicus*. The forewing maculations of these species are very similar, but the lateral lobes of the parameres are distinctive in each (see also *Remarks* under *S. angustus*).

Distributions and associations. Geographic distribution (Fig. 90): Known only from the San Francisco Bay region of California, where it is sympatric with *S. californicus.* Additional collections are necessary to confirm the limits of the range of *S. constrictus.* Temporal distribution: 16 February to 25 October. Altitudinal distribution: no records. Plant associations: *Cupressus macrocarpa, Rhus diversiloba.*

Primary type material examined. Sympherobius constrictus, n. sp. Holotype male. UNITED STATES: California: San Francisco Co., San Francisco (UCB). Verbatim label data: "Lobos Creek / San Francisco, / Calif. II - 16 - 61 / J.Powell Collr.," "ex foliage / Cupressus / macrocarpa," "Holotype / Sympherobius / constrictus Oswald." Condition: excellent, complete. Genitalia in glycerin in microvial pinned below specimen.

Other material examined. 5 male, 13 female paratypes. UNITED STATES: California: Alameda Co.: Berkeley, 2 specimens, 21.viii.1967 (UCB) and 30.iv.1963 (UCB); Berkeley Aquatic Park, 1.v.1967 (UCB). San Francisco Co.: San Francisco, 13 specimens, 7–9.iv.1918 (CAS), 14.viii.1923 (CAS), 8.iii.1960 (CAS) and 25.x.1962 (CAS). Marin Co.: Mill Valley, 21.x.1957 (CAS). No locality, probably San Francisco Bay area, 25.viii.1965 (UCB).

<center>*SYMPHEROBIUS BARBERI* SPECIES COMPLEX</center>

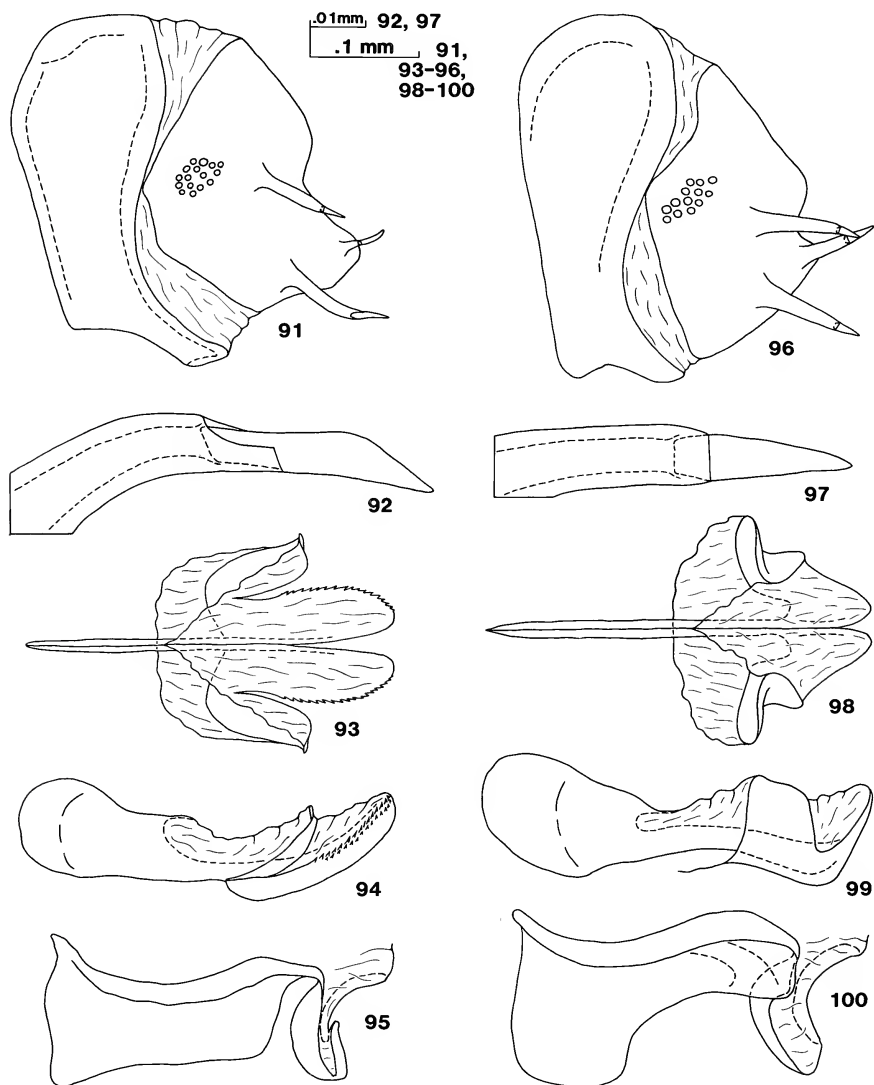<center>*Sympherobius barberi* (Banks)
Figs. 91–95, 103–106, 113</center>

Hemerobius barberi Banks, 1903:241 (OD, A). Holotype female. UNITED STATES: Arizona: Coconino Co., Williams (USNM type #6798).

Sympherobius barberi (Banks): Banks, 1905b (RD, A, Dst, Key, Lst); Banks, 1907b (Lst); Banks, 1911 (Key); Smith, 1925 (Dst); Cole, 1933 (Bic, Bio, Par); Smith, 1934 (L3, L1, E, Bio, Dst, Key); Carpenter, 1940 (RD, A, MG*, W*, Dst, Key); Zimmerman, 1940 (Dst); Froeschner, 1947 (Dst); Parfin, 1952 (Dst); Zimmerman, 1957 (A*, MG*, W*, Bic, Bio, Dst); Nakahara, 1960 (Dst, Tax); Nakahara, 1965a (Dst); Nakahara, 1965b (Dst); Throne, 1971 (Dst); Agnew et al., 1981 (A*, Dst, Key); Klimaszewski et al., [1988] 1987 (Dst, Bio).

Description. Flagellum bicolored, brown proximally, yellow distally. Forewing (Figs. 103–106): Length 3.56–5.69 mm ($\bar{x}$ = 4.61, N = 25). Longitudinal veins pale yellow with brown setal spotting; membrane mottled with irregular light yellowish brown maculations; membrane in area of 2A and 3A with dark maculations; crossveins with or without light brown margining; proximal (very rarely present) and distal radial crossveins absent; darker specimens with membrane maculations darker brown and with most crossveins brown and margined with brown; longitudinal veins with darker setal spotting; membrane hyaline.

Male genitalia: Ectoprocts (Figs. 91, 92): Three unisetose processes present; ventrolateral and ventromedial processes incurved, ventrolateral process abruptly curved; apex of ventrolateral process usually appearing "twisted" (Carpenter, 1940) under low magnification due to its curiously angled setae and odd insertion (Fig. 92), specimens with normal conical, ventrolateral seta have also been examined. Hemigonarcus (Fig. 95): Gonopleuron sinuate, anterior end directed dorsally; gonoplax absent or limited to a small anterodorsal process; extrahemigonarcus wide; hemigonarcal rib absent. Parameres (Figs. 93, 94): Median lobes narrow and elongate,

Figs. 91–100. *Sympherobius barberi*. 91. Ninth tergite and ectoproct, lateral. 92. Apex of ventrolateral ectoproct process. 93–94. Parameres, dorsal and lateral. 95. Gonarcus, lateral. *S. amiculus.* 96. Ninth tergite and ectoproct, lateral. 97. Apex of ventrolateral ectoproct process. 98–99. Parameres, dorsal and lateral. 100. Gonarcus, lateral.

lateral margins prominently toothed; lateral lobes oval in dorsal view, separated from median lobes by a deep incision, apices reflexed; anterior lobes absent; apophysis proxima moderately broad.

Remarks. Sympherobius barberi may be distinguished from *S. amiculus,* which also has bicolored antennae and frequently similar forewing maculations, by the

absence of the distal radial crossvein and the shape of the lateral lobes of the male parameres.

The similarity of forewing maculations in *S. barberi* and many southern *S. amiculus* (compare Figs. 102 and 104) and the occasional presence of specimens with abnormal combinations of male genitalic components suggests the presence of at least occasional hybridization between these species where they are broadly sympatric in the southeastern United States.

Distributions and associations. Geographic distribution (Fig. 113): *Sympherobius barberi* is widely distributed in the New World from approximately 43°N south to Peru, and on several remote Pacific island groups: Galápagos Islands, Revillagigedo Islands and Hawaiian Islands. Temporal distribution: January through December. Altitudinal distribution: 1,300'–6,500' (396 m–1,981 m). Plant associations: *Eupatorium adenophorum* (see Klimaszewski et al., [1988] 1987), *Gillarida* sp., *Juniperus virginiana* (see Throne, 1971), *Lantana camara, Platyopuntia* sp., *Pseudotsuga menziesii* (log), *Quercus chrysolepis, Q. lobata,* oaks (Smith, 1925, 1934), potatoes (Zimmerman, 1940), asparagus fern (Zimmerman, 1957). Prey records: *Aphis medicaqinis* (Aphididae); *Dactylopius* sp., *Dactylopius tomentosus* (Dactylopiidae); *Aonidiella aurantii* (Diaspididae); *Pseudococcus* sp., *Pseudococcus citri* (see Cole, 1933), *Pseudococcus longispinus* (see Zimmerman, 1940), *Pseudococcus adonidum* (see Zimmerman, 1957) (Pseudococcidae); mealybugs (Klimaszewski et al., [1988] 1987).

Primary type material examined. Sympherobius barberi Banks. Holotype female. Verbatim label data: "Williams / 21.7 Ar," "HSBarber / Collector," "Type / No 6798 / U.S.N.M.," "Hemerobius / barberi / type Bks." Condition: good, tips of antennae missing, otherwise complete, wings spread.

Other material examined. 443 specimens. MEXICO: Baja California Norte, Baja California Sur, Chiapas, Coahuila, Oaxaca, Puebla, Revillagigedo Islands [Socorro and Clarion Is.], Sonora, Tamaulipas; PERU; UNITED STATES: Alabama, Arkansas, Arizona, California, Colorado, Florida, Iowa, Illinois, Kansas, Louisiana, Maryland, Mississippi, North Carolina, New Jersey, Oklahoma, Oregon, Pennsylvania, South Carolina, Texas, Utah, Virginia. Institutions: AMNH, ASUT, CAS, CSU, CU, INHS, ISU, LACM, MCZ, MSU, OKS, OSU, OSUC, PMY, SMEK, TAMU, UAT, UCB, UCD, UCR, UMSP, USNM. Also recorded from ECUADOR: Galápagos Islands; MEXICO: Morelos, Nuevo Leon and UNITED STATES: Hawaii, Minnesota, Missouri, New Mexico, Ohio, Wisconsin (Nakahara, 1965b—Morelos, Nuevo Leon; Zimmerman, 1957—Hawaii (introduced); Parfin, 1952—Minnesota; Froeschner, 1947—Missouri; Carpenter, 1940—New Mexico, Ohio; Throne, 1971—Wisconsin; Klimaszewski et al., [1988] 1987—Galápagos Islands).

Sympherobius umbratus (Banks)
Figs. 64, 107–112

Hemerobius umbratus Banks, 1903:242 (OD, A, MG*). Holotype male. UNITED
    STATES: Arizona: Coconino Co., Williams (USNM type #6799): Banks, 1904a
    (Dst).
Sympherobius umbratus (Banks): Banks, 1905b (RD, A, MG*, Dst, Key, Lst); Banks,
    1907b (Lst); Banks, 1911 (Key); Carpenter, 1940 (RD, A, MG*, Dst, Key, Tax);
    Froeschner, 1947 (Dst).
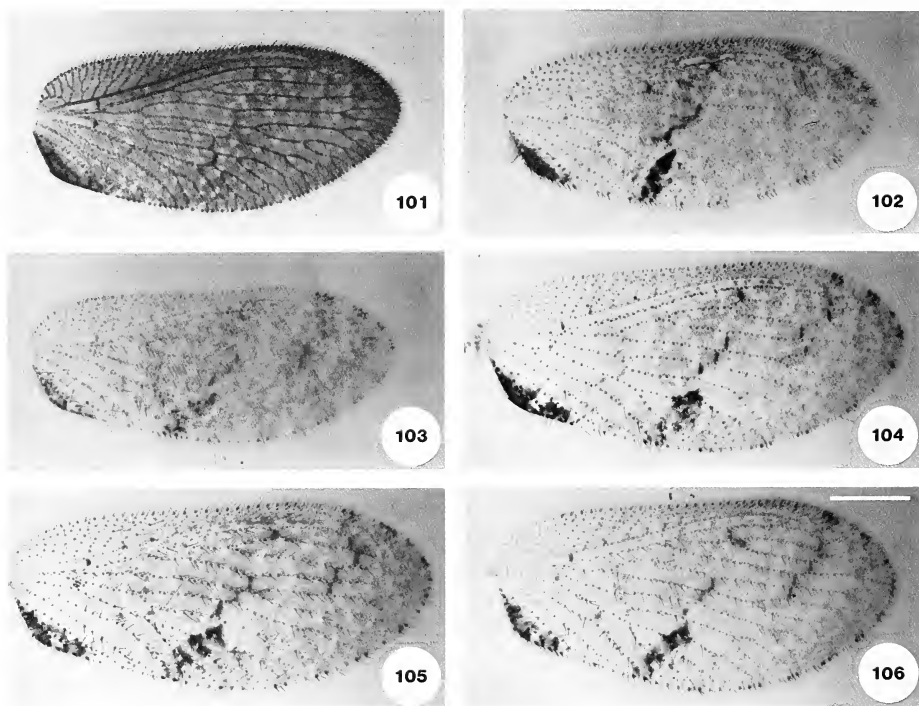
Figs. 101–106. Forewings of *Sympherobius*. 101. *S. amiculus*, a specimen from New York. 102. *S. amiculus*, a specimen from North Carolina. 103. *S. barberi*, a specimen with normal venation. 104–106. *S. barberi*, three specimens showing different anomalous arrangements of the branches of the radius. Scale bar = 1 mm. All figures to same scale.

Sympherobius gracilis Carpenter, 1940:231 (OD, A, MG*, Key). Holotype male.
    UNITED STATES: North Carolina: Wake Co., Raleigh (MCZ type #23,676). **New Synonym.**

Description. Antennae: Scape and pedicle brownish yellow; flagellum brownish yellow proximally, brownish distally. Forewings (Fig. 64): Length 4.19–5.20 mm ($\bar{x}$ = 4.59, N = 7). Veins monochromatic dark brown; veins narrowly margined with brown; membrane within cells brown bordered by a narrow band of hyaline or lighter brown; central region of membrane in cells of discal area lighter brown than surrounding membrane; proximal radial crossvein absent, distal radial crossvein present (occasionally absent or joining R1+2+3 to R4+5).

    Male genitalia: Ectoprocts (Figs. 107, 108): Three processes present; dorsolateral and ventromedial processes unisetose; ventrolateral process bisetose; Carpenter (1940) indicates incorrectly that the ventromedial process is also "furcate"; ventromedial process incurved. Hemigonarcus (Fig. 111): Gonopleuron sinuate, anterior end directed dorsally; gonoplax absent; extrahemigonarcus an angular lobe anteriorly, narrowed posteriorly; anteroventral margin of extrahemigonarcus curved toward gonarcus midline; hemigonarcal rib absent. Parameres (Figs. 109, 110): Lateral lobes

prominent, curving dorsally and medially, anterior margin flared laterally; anterior lobes absent; apophysis proxima broad.

Remarks. Carpenter (1940:230, Figs. 30A, 30B) incorrectly figured the dorsolateral process of the ectoproct as "furcate." The ventrolateral process is actually "furcate" (i.e., bisetose). For a discussion of similar species see *Remarks* under *S. amiculus.*

Distributions and associations. Geographic distribution (Fig. 112): Eastern United States; one outlier from Arizona has also been examined. Temporal distribution: 16 March through 5 September. Altitudinal distribution: no records. Plant associations: no records.

Primary type material examined. Sympherobius umbratus Banks. Holotype male. Verbatim label data: "Williams / 10-6 Ar," "HSBarber / Collector," "Type / No 6799 / U.S.N.M.," "Hemerobius / umbratus Bks type." Condition: excellent, complete, wings spread, abdomen and dissected genitalia in glycerin in microvial pinned below specimen.

Sympherobius gracilis Carpenter. Holotype male. Verbatim label data: "Raleigh. NC / 11 - VI - 34 / R.W. Leiby," "23," "M.C.Z. Type 23676," "Sympherobius / gracilis Carp. / det. F.M. Carpenter." Condition: poor, left midleg, left hindleg, right foretarsus and left hindwing missing. Right hindwing and left forewing dry in microvial pinned below specimen. Genitalia in glycerin in another microvial pinned below specimen.

Other material examined. 20 specimens. UNITED STATES: Arkansas: Pulaski Co.: Little Rock, 12.vi.1943 (LACM). Washington Co.: Devil's Den St. Pk., 4 specimens, 8.vi–19.vii.1966 (USNM). Georgia: Clarke Co.: Stonehenge, 5.ix.1973 (UGA); 5 mi. W. Athens, 7–13.viii.1977 (UGA). Missouri: Boone Co.: Ashland, 6 specimens, 31.vii.–17.viii.1968 (UMC). North Carolina: Mecklenburg Co.: Matthews, 30.iii.1967 (CU). Polk Co.: Tryon, 21.vi. (USNM). Oklahoma: Sequoyah Co.: Tenkiller Lake, 3 mi. W Blackgum, 6–9.vii.1979 (USNM). Pennsylvania: Allegheny Co.: Edgewood, 1–2.ix.1957 (CMP). Beaver Co.: Darlington, 8.vii.1971 (CMP). South Carolina: Charleston Co.: Wedge Plantation, McClellanville, 16.iii.1968 (PMY). Virginia: Fairfax Co.: Vienna, 20.vi.1939 (USNM). Also recorded from UNITED STATES: New Mexico (Carpenter, 1940). This record seems doubtful.

<center>

*Sympherobius amiculus* (Fitch)
Figs. 1–3, 90, 96–102

</center>

Hemerobius amiculus Fitch, [1855] 1854:799 (OD, A). Holotype female. UNITED STATES, precise locality unknown, probably New York or Illinois (see Carpenter, 1940) (MCZ type #10,449): Hagen, 1861 (RD, A, Dst); Banks, 1892 (Lst); Krüger, 1922 (Tax).

Sympherobius amiculus (Fitch): Banks, 1904b (Dst); Banks,1905b (RD, A, MG*, Dst, Key, Lst); Banks, 1907a (Dst); Banks, 1907b (Lst); Banks, 1911 (Key); Comstock, 1918 (W*); Smith, 1923 (C*, P*, PP*, L3*, L2*, L1, E*, Bio); Smith, 1925 (Dst); Smith, 1934 (Dst, Key); Brimley, 1938 (Dst); Carpenter, 1940 (RD, A, MG*, W*, Dst, Key, Tax); Froeschner, 1947 (Dst); Parfin, 1952 (Dst); Nakahara, 1960 (Dst, Tax); Mann, 1969 (Bio); Throne, 1971 (Dst); Agnew et al., 1981 (A*, W*, Dst, Key).

Palmobius amiculus (Fitch): Needham, 1905 (W*, Tax).

[*Spadobius occidentalis* (Fitch): Needham, 1905 (Tax). Misidentification.]
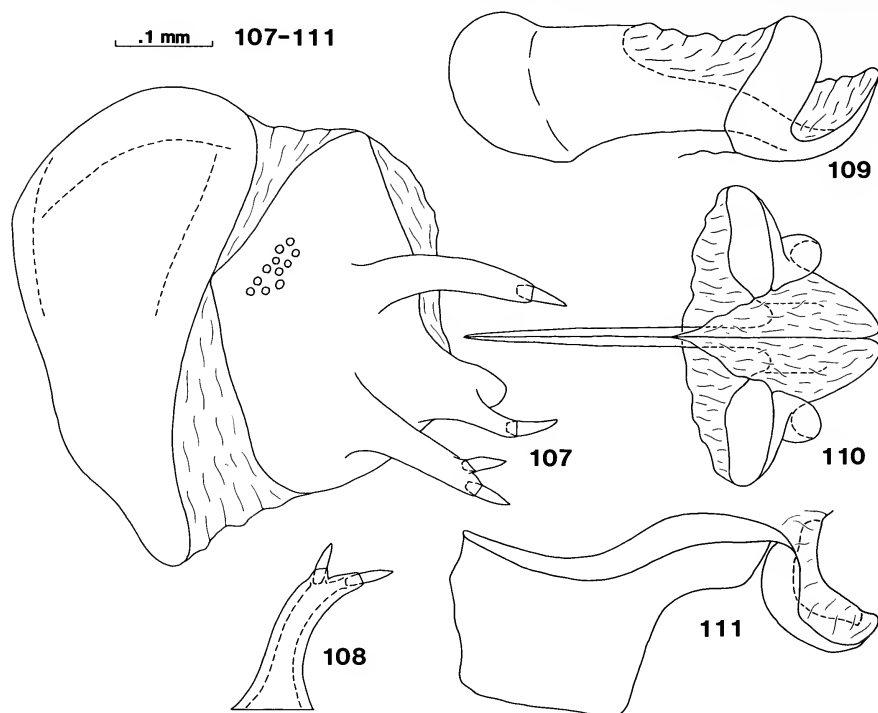
Figs. 107–111. *Sympherobius umbratus.* 107. Ninth tergite and ectoproct, lateral. 108. Ventrolateral ectoproct process. 109–110. Parameres, lateral and dorsal. 111. Gonarcus, lateral.

Sympherobius buenoi Navás, 1912:198 (OD, A, W*). Holotype male. UNITED
  STATES: New York: Westchester Co., White Plains (not examined, repository
  unknown): Carpenter, 1940 (Tax).

Description. Antennae: Flagellum bicolored, dark brown proximally, yellowish
brown distally. Forewing (Figs. 101, 102): Length 3.43–5.64 mm ($\bar{x} = 4.44$, N = 25).
Proximal radial crossvein absent; distal radial crossvein present (rarely absent). *Sympherobius amiculus* exhibits considerable interspecific variation in forewing coloration. At least part of this variation appears correlated with a latitudinal morphocline
of darker northern forms and lighter southern forms. Specimens from southern latitudes tend to display the following characteristics (Fig. 102): (1) longitudinal veins
yellowish with prominent brown setal spotting, (2) membrane largely yellowish hyaline with scattered light brown maculations and (3) inner gradate crossveins broadly
margined with dark brown. Forewing frequently with a dark band extending across
the inner gradate series from the radius to the posterior margin of the wing; most
other crossveins unmargined. Northern specimens tend to display the following corresponding characters (Fig. 101): (1) longitudinal veins predominantly light brown,
setal spotting present but not prominent, (2) membrane largely brownish with hyaline
maculations and (3) inner gradate series margined or unmargined but forewing without a prominent dark band.

Male genitalia: Ectoprocts (Figs. 96, 97): Three incurved unisetose processes present. Hemigonarcus (Fig. 100): Gonopleuron sinuate, anterior end directed dorsally; gonoplax absent; extrahemigonarcus broadly lobate anteriorly, narrowed posteriorly; hemigonarcal rib present, unforked. Parameres (Figs. 98, 99): Lateral lobes dorsally revolute, anterior margin flared laterally; anterior lobes absent; apophysis proxima moderately broad.

Remarks. The forewing maculations and bicolored antennae of *S. amiculus* are similar to those of *S. barberi,* but in *S. amiculus* the distal radial crossvein is present, in *S. barberi* this crossvein is absent. *Sympherobius umbratus,* the only other species in which the distal radial crossvein is present, may be distinguished from *S. amiculus* by its dark forewing membrane and bisetose ventrolateral ectoproct process. See also *Remarks* under *S. barberi.*

Distributions and associations. Geographic distribution (Fig. 90): *Sympherobius amiculus* is the most frequently collected species throughout southeastern Canada and the eastern United States. Its primary distribution extends west to about the 100th meridian. I have also seen single male specimens from Arizona (Maricopa Co.) and Colorado (Larimer Co.). Temporal distribution: 15 January through 11 November. Altitudinal distribution: no records. Plant associations: *Pinus banksiana, P. taeda, P. virginiana* and "Jap. Holly." Also recorded from apple and oak (Smith, 1923; 1925), *Pinus virginiana* (see Froeschner, 1947), conifers, oaks and vineyards (Agnew et al., 1981). Prey records: Mann (1969:12, 142) reported '*S. amiculus*' [=*barberi* ?] as an important predator of cactus infesting *Dactylopius* sp. (Dactylopiidae) in Texas.

Primary type material examined. Hemerobius amiculus Fitch. Holotype female. Verbatim label data: "3964," "Type / 10449," "Hemerobius / amiculus." Condition: poor, moldy, right wings and pieces of several legs missing. Genitalia in glycerin in microvial pinned below specimen.

Other material examined. 365 specimens. CANADA: Quebec; UNITED STATES: Alabama, Arizona, Arkansas, Colorado, Connecticut, District of Columbia, Florida, Georgia, Illinois, Iowa, Kansas, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Nebraska, New Jersey, New York, North Carolina, Ohio, Pennsylvania, South Carolina, Tennessee, Texas, Vermont, Virginia, West Virginia, Wisconsin. Institutions: AMNH, ASUT, CAS, CMP, CSU, CU, FEM,INHS, ISU, LACM, LSU, MCZ, MSU, NCSR, OSU, OUSC, SMEK, TAMU, UAF, UAT, UCB, UCD, UGA, UMAA, UMC, UMSP, UNH, USNM, UWM, VPI, WSU. Also recorded from CANADA: Nova Scotia, Ontario and UNITED STATES: New Hampshire, Oklahoma (Carpenter, 1940).

PHYLOGENETIC RELATIONSHIPS

The relative phylogenetic relationships among the 17 *Sympherobius* species of America north of Mexico are inferred below based on a cladistic analysis. Cladistic analyses utilize hypotheses of synapomorphic (shared derived) character states in conjunction with a parsimony criterion to infer the relative recency of common ancestry among a set of taxa under scrutiny (Hennig, 1966; Wiley, 1981).

In this analysis, the method of outgroup comparison (Watrous and Wheeler, 1981) has been used, in most cases, to determine polarities of character states. Identification of appropriate outgroups proved difficult due to the lack of a well-substantiated prior
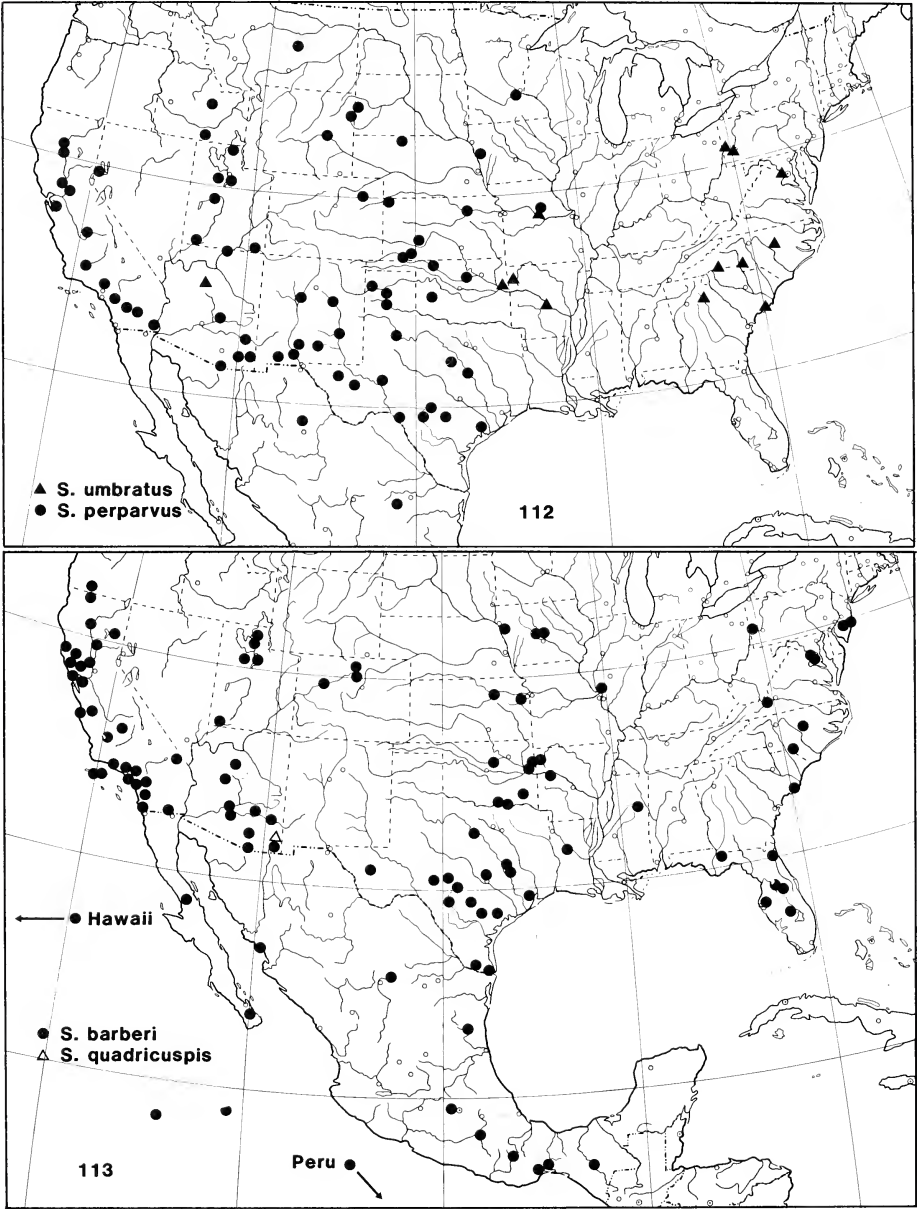
Figs. 112, 113.   Geographic distributions of Nearctic *Sympherobius*. Only verified records plotted.

hypothesis of hemerobiid intergeneric relationships. Selections for outgroup taxa are justified below.

The hemerobiid family group taxa proposed by Comstock (1918), Krüger (1922), Navás (1933) and Nakahara (1960), having been based on either plastic venational characters or a single character of the male genitalia, were considered insufficiently justified by Tjeder (1961). Following Tjeder, most subsequent authors have recognized no suprageneric taxa within the family. Consequently, intergeneric relationships within the Hemerobiidae are almost entirely unresolved; and the phylogenetic affinities of *Sympherobius* remain unclear.

Earlier authors suggested that the phylogenetic affinities of *Sympherobius* may lie near the genus *Nomerobius* (see Penny and Monserrat, [1985] 1983:894), or *Psectra* or *Notiobiella* (see Comstock, 1918:179). These hypotheses were based primarily on the shared presence in these genera of only two oblique branches of the forewing radius, a character also found in several other hemerobiid genera (e.g., *Anapsectra, Carobius, Kimminsiella, Neosympherobius* and *Zachobiella*) and probably plesiomorphic within the family.

An examination of representative species (or illustrations) of these and most other hemerobiid genera has revealed the presence of a pseudomediuncus only in the genera *Neosympherobius, Nomerobius* and *Sympherobius*. Based on the presence of a pseudomediuncus and also the shared, and apparently derived, presence of a digitiform process located near the ventromedial margin of the male ectoproct, these three genera appear to form a monophyletic group (Fig. 114), informally named here the *Nomerobius* genus group. A pair of synapomorphies (losses of the distal radial crossvein and mediuncus) support the monophyly of '*Neosympherobius + Sympherobius*.' A further pair of purported synapomorphies (pseudomediuncus bipartite and basi-pseudomediuncus dished and with flared lateral margins) support the monophyly of *Sympherobius* itself.

As the putative sister groups, respectively, of *Sympherobius* and '*Neosympherobius + Sympherobius*,' *Neosympherobius* and *Nomerobius* have been used as outgroup taxa in the present analysis. In the succeeding paragraphs I present the 23 binary characters used in the cladistic analysis. Where not based on outgroup comparison to *Nomerobius* and *Neosympherobius* (see Table 1), the rationale for assigning character state polarities (0 = plesiomorphic, 1 = apomorphic) is given.

Characters

Venation

1. Proximal radial crossvein (joining R1+2+3 to R4+5): (0) absent, (1) present. See discussion under character 2.
2. Distal radial crossvein (joining R2+3 to R4+5): (0) present, (1) absent. The distal radial crossvein is present in *Nomerobius* and two species of *Sympherobius,* absent in *Neosympherobius* and other *Sympherobius.* I assume presence of the distal radial crossvein to be plesiomorphic. This state is more widely distributed among hemerobiid genera possessing two oblique radial branches of the forewing (e.g., *Nomerobius, Psectra, Anapsectra, Notiobiella, Zachobiella* and *Kimminsiella*) than is the alternate state of absence (*Neosympherobius, Carobius*).

Carpenter (1940) demonstrated the taxonomic utility of the "radial crossvein" in diagnosing Nearctic *Sympherobius*. Presented as a single homologous crossvein of variable location, Carpenter identified three positional states for the "radial crossvein": (1) joining $R1+2+3$ to $R4+5$, (2) absent, or (3) joining $R2+3$ to $R4+5$. In a fourth condition recently found in some species of the Oriental-Australian genus *Zachobiella* and in several undescribed species related to the Australian genus *Carobius* (T. R. New, pers. comm.) crossveins are present joining both the $R1+2+3$ to $R4+5$ [state (1) above] and the $R2+3$ to $R4+5$ [state (3) above]. This additional condition strongly suggests that Carpenter's "radial crossvein" may consist of two separate non-homologous crossveins. Though this fourth condition is not presently known to occur in species of the *Nomerobius* genus group, its possibility cannot be ruled out as a transitional state. For this reason, contrary to Carpenter's (1940) presentation, crossveins in the positional states (1) and (3) above are interpreted in this work as two independent characters: the proximal (Fig. 4, prc) and distal radial crossveins (drc) respectively.

Females

3. Tergite 8, lateral ends: (0) widely separated ventrally, (1) adjacent or fused ventrally. The state of this character in *Neosympherobius* is unknown.

Males

4. Tergite 9, anterodorsal emargination: (0) absent or shallow, (1) deep.
5. Ectoproct, ventromedial process: (0) absent, (1) present. See discussion under character 7.
6. Ectoproct, ventrolateral process: (0) absent, (1) present. See discussion under character 7.
7. Ectoproct, dorsolateral process: (0) absent, (1) present.

Within *Sympherobius* when a single male ectoproct process is present it always arises from near the ventromedial margin of the ectoproct. When a pair of processes are present they are laterally adjacent and located ventrally on the ectoproct; the inner process occupying a position near the ventomedial margin of the ectoproct. When a third process is present it arises near the middle of the ectoproct dorsal to the ventrals, which retain the relative positions described under the two process condition. The constancy of the relative positions of these processes in all species strongly supports the hypothesis that processes with the same relative positions are homologous.

Independent confirmation of the homology of individual ectoproct processes found in *Sympherobius* with similar processes found on the ectoprocts of *Neosympherobius* and *Nomerobius* is lacking. Applying the relative positional hypothesis used to determine process homology within *Sympherobius,* I have assumed that the single process of *Nomerobius* and *Neosympherobius* ectoprocts is the homologue of the ventromedial process of *Sympherobius.* In *Nomerobius* this process is in fact located in a ventromedial position, but in *Neosympherobius* the lone process arises somewhat more laterally. The ectoproct of *Nomerobius* also possesses an additional short process located dorsad and laterad to the ventromedial process. This process consists of a thick-

ened, elongate seta borne on a short, narrow chalaza and is not considered to be a homologue of the digitiform processes of the *Nomerobius* genus group which terminate in a spinate or peg-like modified seta.

8. Ectoproct, dorsomedial prominence: (0) absent, (1) present. The dorsomedial prominence is absent in *Nomerobius, Neosympherobius* and most *Sympherobius.* The dorsomedial prominence differs from other *Sympherobius* ectoproct processes by lacking a terminal modified seta (though it may bear normal seta laterally, compare Figs. 56 and 97). The lack of a terminal modified seta and the dorsomedial position of the dorsomedial prominence support the hypothesis that it is not a homologue of the non-digitiform chalaza found on the ectoprocts of male *Nomerobius.*

9. Ectoproct, ventromedial process, terminal calyx rim: (0) not sheath-like, (1) sheath-like.

10. Ectoproct, ventromedial process, shape of terminal seta: (0) peg-like, (1) spinose.

11. Ectoproct, ventromedial process, shape of terminal seta: (0) not grooved, (1) grooved.

12. Ectoproct, ventrolateral process, number of modified setae: (0) one, (1) two. *Nomerobius* and *Neosympherobius* lack a ventrolateral process. A single modified seta is assumed to be the plesiomorphic state. This interpretation is supported by observing that the ventromedial process and, when present, the dorsolateral process always terminates in a single modified seta. This is also the most common state for the ventrolateral process.

13. Parameres, anterior lobes: (0) absent, (1) present.

14. Parameres, apices of anterior lobes: (0) narrow, (1) broad. *Nomerobius* and *Neosympherobius* lack anterior paramere lobes. The polarity of this character was determined by congruence with other polarized characters.

15. Parameres, lateral lobes: (0) absent, (1) present.

16. Parameres, lateral lobe curvature: (0) distal margins curved dorsally, (1) distal margins dorsally revolute. *Nomerobius* and *Neosympherobius* lack lateral paramere lobes. The polarity of this character was determined by congruence with other polarized characters.

17. Parameres, lateral lobes, longitudinal rib or ridge: (0) absent, (1) present. *Nomerobius* and *Neosympherobius* lack lateral paramere lobes. The polarity of this character was determined by congruence with other polarized characters.

18. Gonarcus, gonopleuron shape: (0) approximately linear, (1) turned up anteriorly.

19. Gonarcus, gonopleuron shape: (0) approximately linear, (1) turned down anteriorly.

20. Pseudomediuncus: (0) absent, (1) present. *Nomerobius, Neosympherobius* and *Sympherobius* are jointly characterized by the presence of a pseudomediuncus. I am unaware of any other hemerobiid genera possessing a comparable sclerotized structure lying along the dorsal midline of the paragonarcal membrane.

21. Pseudomediuncus, form: (0) entire, (1) bipartite. In *Nomerobius* and *Neosympherobius* the pseudomediuncus is a continuous strip of weakly sclerotized cuticle. In *Sympherobius* the pseudomediuncus is clearly divided into a pair

Table 1. Character state matrix for Nearctic *Sympherobius* and outgroups used to generate cladogram shown in Figure 114. Character numbers refer to characters discussed in text. Matrix symbols: 0, plesiomorphic state; 1, apomorphic state; *, state unknown; —, character inapplicable.

Taxon												Character number											
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Nomerobius	0	0	0	0	1	0	0	0	0	0	0	—	0	—	0	—	—	0	0	1	0	0	0
Neosympherobius	0	1	*	0	1	0	0	0	0	0	0	—	0	—	0	—	—	0	0	1	0	0	1
S. perparvus	0	1	0	0	1	0	0	0	1	1	0	—	1	1	0	—	—	0	0	1	1	1	1
S. beameri	0	1	0	0	1	0	0	0	1	1	0	—	1	1	0	—	—	0	0	1	1	1	1
S. arizonicus	0	1	0	0	1	0	0	0	1	1	1	—	1	0	0	—	—	0	0	1	1	1	1
S. killingtoni	0	1	0	0	1	0	0	0	1	1	1	—	1	0	0	—	—	0	0	1	1	1	1
S. pictus	0	1	1	0	1	0	0	0	0	0	0	0	0	—	0	—	—	0	0	1	1	1	1
S. similis	1	1	*	0	1	1	*	0	0	0	0	0	0	0	0	—	—	0	0	1	1	1	1
S. occidentalis	1	1	1	0	1	1	0	0	0	0	0	0	1	—	0	—	—	0	1	1	1	1	1
S. limbus	0	1	1	0	1	1	1	0	0	0	0	0	0	—	0	—	—	—	0	1	1	1	1
S. distinctus	0	1	*	1	1	1	1	1	0	0	0	0	0	—	1	0	0	0	0	1	1	1	1
S. angustus	1	1	1	1	1	1	1	1	0	0	0	0	0	—	1	0	0	0	1	1	1	1	1
S. quadricuspis	1	1	*	0	1	1	1	0	0	0	0	1	0	—	1	0	0	0	1	1	1	1	1
S. bifasciatus	1	1	*	1	1	1	1	0	0	0	0	0	0	—	1	0	1	—	1	1	1	1	1
S. californicus	1	1	1	1	1	1	1	0	0	0	0	0	0	—	1	0	1	—	1	1	1	1	1
S. constrictus	1	1	*	1	1	1	1	0	0	0	0	0	0	—	1	0	0	—	—	1	1	1	1
S. barberi	0	1	1	1	1	1	1	0	0	0	0	0	0	—	1	1	0	1	—	1	1	1	1
S. umbratus	0	0	1	0	1	1	1	0	0	0	0	1	0	—	1	1	0	1	—	1	1	1	1
S. amiculus	0	0	1	0	1	1	1	0	0	0	0	0	0	—	1	1	0	1	—	1	1	1	1

of sclerites which articulate at a membranous or weakly sclerotized region between them.

22. Basipseudomediuncus (or base of undivided pseudomediuncus), form: (0) flat and narrow, strap-like, (1) lateral margins splayed and recurved forming a shallow basin. In *Nomerobius* and *Neosympherobius* the base of the pseudomediuncus is a narrow strap-like sclerite. In *Sympherobius* the lateral margins of the basipseudomediuncus are produced and arched to form a shallow concave basin into which the distopseudomediuncus may seat.

23. Mediuncus: (0) present, (1) absent. A mediuncus is present in *Nomerobius,* but absent in *Neosympherobius* and *Sympherobius.* Based on the presence of a mediuncus in most other Neuroptera, I consider the former state plesiomorphic.

Analysis and Results

The character state distributions of the outgroup and ingroup taxa are summarized in Table 1. Unknown characters and characters inapplicable to some species (i.e., characters involving subsequent modifications to structures themselves not present in that species) were coded as missing data. A single most parsimonious tree topology (Length = 28 steps, CI = .75) was derived from these data by employing the Mulpars and Global Branch Swapping options of the Phylogenetic Analysis Using Parsimony (PAUP) computer program (Swofford, 1985). This tree and its supporting characters are illustrated in Figure 114.

Discussion

Figure 114 depicts the hypothesized phylogenetic relationships among the 17 Nearctic species of *Sympherobius.* In the discussion below four major lineages within *Sympherobius* displayed on this cladogram are identified, informally named and briefly discussed. Numbers enclosed in square brackets in the following discussion refer to the preceding character listing.

The basal dichotomy within *Sympherobius* separates the *S. perparvus* and *S. pictus* species groups. Gurney (1948) proposed the *S. perparvus* species group for the species *S. beameri, S. killingtoni* and *S. perparvus* based on the single digitiform process of the male ectoprocts shared by these species. Gurney further suggested that *S. arizonicus* and *S. pictus,* the males of which were unknown at that time, might also belong to this group. The male of *S. arizonicus* was subsequently described by MacLeod (1963) and confirmed as a member of the *perparvus* group. The male of *Sympherobius pictus,* described here for the first time, possesses a single ectoproct process but, though closely related to, is clearly not a member of the *S. perparvus* species group clade. Since the male ectoprocts of *S. pictus* and the four species of the *S. perparvus* group each bear a single digitiform process, the single character proposed by Gurney is no longer tenable as a synapomorphy of the *S. perparvus* group. My analysis suggests the following three characters as synapomorphies of this group: (1) the rim of the calyx into which the terminal seta of the ventromedial ectoproct process inserts is elongate and sheath-like [9], (2) the terminal seta of the ventromedial process is spinose, not peg-like [10] and (3) the presence of anterior paramere lobes [13]. The last character is independently derived in *S. occidentalis.* With mean forewing lengths
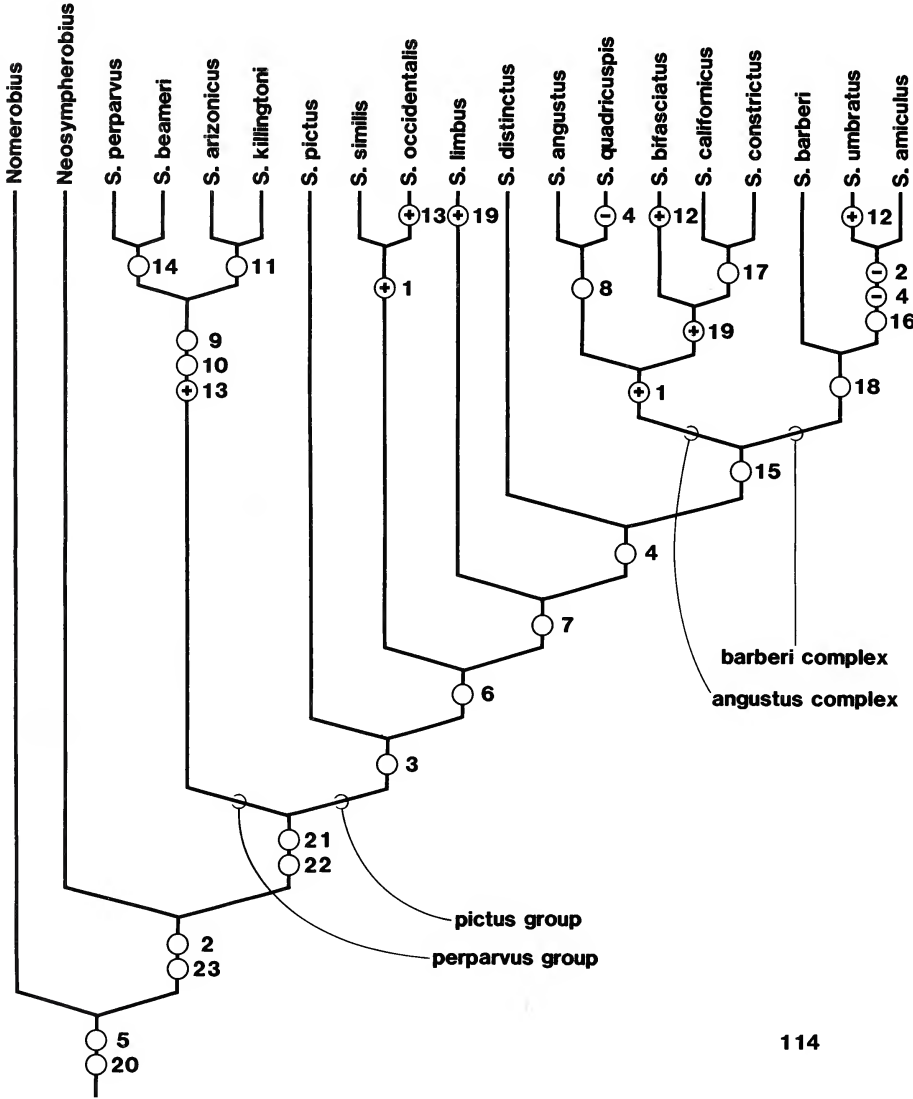
Fig. 114. Cladogram of the Nearctic species of *Sympherobius*. Numbers refer to characters discussed in the text. Autapomorphies of individual species are omitted except where they are part of a homoplasious complex (e.g., characters 12, 13). Symbols: +, convergent character; −, character reversal.

of 3.77–4.07 mm, most of the smallest Nearctic *Sympherobius* species are members of the *S. perparvus* group.

The *S. perparvus* group appears to occupy an isolated position within *Sympherobius*. None of the approximately 20 Palearctic and South and southern Central Amer-

ican species examined to date possess the synapomorphies of the *S. perparvus* group. However, some Mexican forms not treated in this revision may belong to this group.

All four species of the *S. perparvus* group occur in arid regions of the southwestern United States. *Sympherobius perparvus, S. killingtoni* and *S. arizonicus* have also been recorded from adjacent northern Mexico. Each of the four species of this group further exhibit northerly range extensions into one or more of the following regions: (1) the Central Valley of California, (2) the Great Basin of the western United States and/or (3) the Great Plains of the central United States.

Sympherobius pictus and the remaining Nearctic species are placed in a new species group, the *S. pictus* group. This group is characterized by the lateral ends of female tergite 8 being adjacent or fused on the venter of the abdomen [3]. The *S. angustus* (5 species) and *S. barberi* (3 species) complexes are united by the shared presence of lateral lobes of the parameres [15]. The five species of the *S. angustus* complex, *S. angustus, S. quadricuspis, S. bifasciatus, S. californicus* and *S. constrictus,* are generally larger species (mean forewing lengths: 4.32–5.63 mm) characterized by the presence of a proximal radial crossvein [1]. The three species of the *S. barberi* complex, *S. barberi, S. umbratus* and *S. amiculus,* are intermediate in size (mean forewing lengths: 4.44–4.61 mm) and are characterized by the distally upturned gonopleuron [18].

The *S. pictus* group is diverse with respect to male ectoproct spination, parameral lobation and radial crossvenation. It seems likely that the phylogenetic affinities of most extralimital species will later be found to be with this group.

The male ectoprocts of most extralimital species examined from the Palearctic region and the Americas south of the United States possess two or three digitiform processes (i.e., the apomorphic states of characters [5] and [6] or [5], [6] and [7]), and lack lateral lobes on the parameres (i.e., the plesiomorphic state of character [15]); the phylogenetic affinities of such species will most likely be with Nearctic species found in the pectinate basal stem of the *S. pictus* group. Some South American species possess three digitiform ectoproct processes (i.e., the apomorphic states of characters [5], [6] and [7]), and lateral lobes on the parameres (i.e., the apomorphic state of character [15]); the affinities of these species may be with the *S. angustus* and/or *S. barberi* complex(es). Since species apparently belonging to the *S. pictus* group are well represented outside the Nearctic region, any analysis of biogeographic patterns within this group at this time would be premature.

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APPENDIX 1

Synonymical List of World *Sympherobius* species

The following list contains all species-group names (valid, junior synonyms, nomina nuda and nomina dubia) which are currently associated with the generic name *Sympherobius*. 54 valid species-group names (in bold italics in the alphabetical sequence below) and 45 invalid or unavailable species-group names (in non-bold italics) are listed. Complete bibliographic citations for each name can be found in the Literature Cited. Each species-group name is given in its original combination. No attempt has been made to catalogue the subsequent combinations of each species-group name. An indication of the known geographic distribution of each valid species is also given. For additional information on non-Nearctic species see the works cited at the beginning of this paper. *Sympherobius exiguus* (Navás) and *S. marginata* (Kimmins) are new combinations. "*Sympherobius thaumasta* Navás (1915)," cited by Penny ([1978] 1977: 33), is a *lapsus calami* for *Symphrasis thaumasta* Navás, 1915e:197 (Mantispidae).

Synonymical List

amazonica Penny and Monserrat, [1985] 1983: Brazil.
    Sympherobius amazonica Penny and Monserrat, [1985] 1983:889.
amiculus (Fitch, [1855] 1854): Southeastern Canada, eastern, central and southwestern United States.
    Hemerobius amiculus Fitch, [1855] 1854:799.
    Sympherobius buenoi Navás, 1912:198.
amicus (Navás in Silvestri, 1915). See *fallax* Navás, 1908.
angustus (Banks, 1904): Southwestern Canada, western United States south to southern Mexico.
    Hemerobius angustus Banks, 1904a:102.
    Sympherobius tristis Navás, 1914a:15.
    Sympherobius stangei Nakahara, 1960:16.
    Sympherobius brunneus Nakahara, 1965a:207.
ariasi Penny and Monserrat, [1985] 1983: Brazil.
    Sympherobius ariasi Penny and Monserrat, [1985] 1983:890.
arizonicus Banks, 1911: Arizona and southern California south to southern Mexico.
    Sympherobius arizonicus Banks, 1911:346.
axillaris Navás, [1928] 1927: Mexico.
    Sympherobius axillaris Navás, [1928] 1927:321.
barberi (Banks, 1903): Southern and eastern United States south to Peru, Galápagos Islands, Hawaiian Islands (introduced), Revillagigedo Islands.
    Hemerobius barberi Banks, 1903:241.
beameri Gurney, 1948: Southwestern United States.
    Sympherobius beameri Gurney, 1948:220.
bellus Navás, 1911. See *pygmaeus* (Rambur, 1842).
bifasciatus Banks, 1911: Southwestern United States, northern Mexico.
    Sympherobius bifasciatus Banks, 1911:347.
bisignatus (Krüger, 1922): Unknown.
    Spadobius bisignatus Krüger, 1922:171 Nomen Nudum.
blanchardi (Navás, 1930): Chile.
    Coloma blanchardi Navás, 1930b:19.
brincki Tjeder, 1961. See *smithersi* Nakahara, 1960.
brunneus Nakahara, 1965. See *angustus* (Banks, 1904).
buenoi Navás, 1912. See *amiculus* (Fitch, [1855] 1854).
californicus (Banks, 1905). See *californicus* Banks, 1911.

californicus Banks, 1911: California and northwestern Mexico.

    Hemerobius californicus Banks, 1905a:90 Nomen Nudum.

    Sympherobius californicus Banks, 1911:346.

carpathicus Kis, 1965. See *pellucidus* (Walker, 1853).

catalaunicos (Navás, 1930). See *elegans* (Stephens, 1836).

catalaunicus (Navás, 1930). See *elegans* (Stephens, 1836).

coccophagus (Göszy, 1852): Sardinia.

    Hemerobius coccophagus Göszy, 1852:346 Nomen Dubium (= *Sympherobius pygmaeus* ?).

conspersus Navás, 1908. See *pygmaeus* (Rambur, 1842).

constrictus Oswald n. sp.: California.

    Sympherobius constrictus Oswald n. sp.

dilutus Nakahara, 1960: Japan.

    Sympherobius dilutus Nakahara, 1960:19.

distinctus Carpenter, 1940: Arizona and Colorado.

    Sympherobius distinctus Carpenter, 1940:238.

domesticus Nakahara, 1954: Japan.

    Sympherobius domesticus Nakahara, 1954:43.

elegans (Stephens, 1836): Europe, USSR.

    Hemerobius elegans Stephens, 1836:113.

    Hemerobius marshami Stephens, 1836:114.

    Hemerobius paucinervis Zetterstedt, 1840:1050.

    Hemerobius striatellus Klapálek, 1905:725.

    Sympherobius venustus Navás, 1908a:27.

    Hemerobius vicentei Navás, 1914b:34.

    Nefasitus catalaunicus Navás, 1930a:161.

    Nefasitus catalaunicos [sic] Navás, 1930a:162 (name unavailable, an incorrect original spelling of *N. catalaunicus* Navás).

exiguus (Navás, 1908): Canary Islands.

    Micromus exiguus Navás, 1908b:407 New Combination.

fallax Navás, 1908: Southern Europe, Middle East and northern Africa.

    Sympherobius fallax Navás, 1908b:408.

    Sympherobius schmitzi Navás, 1908b:409.

    Sympherobius tenellus Navás, 1908a:25.

    Nefasitus amicus Navás in Silvestri, 1915:332.

    Sympherobius sanctus Tjeder, 1939:43.

fortini Lacroix, 1924. See *pygmaeus* (Rambur, 1842).

fuscescens (Wallengren, 1863): Europe, Asia and Japan.

    Hemerobius fuscescens Wallengren, 1863:20.

    Hemerobius inconspicuus McLachlan, 1868:177.

    Niremberge limpida Navás, 1909:377.

fuscinervis Kozhantshikov, 1956: Turkestan.

    Sympherobius fuscinervis Kozhantshikov, 1956:700, 705.

gayi Navás, 1910: Chile.

    Sympherobius gayi Navás, 1910b:237.

gracilis Carpenter, 1940. See *umbratus* (Banks, 1903).

gratiosus Navás, 1908. See *pygmaeus* (Rambur, 1842).

humilis Navás, 1914: Paraguay.

    Sympherobius humilis Navás, 1914c:226.

hyalinus Monserrat, 1976. See *klapaleki* Zelený, 1963.

impar Tjeder, 1961. See *smithersi* Nakahara, 1960.

inconspicuus (McLachlan, 1868). See *fuscescens* (Wallengren, 1863).

innoceus Steinmann, 1965: Argentina.
    Sympherobius innoceus Steinmann, 1965:567.
insulanus Banks, 1938: Cuba.
    Sympherobius insulanus Banks, 1938:292.
intervenalis Banks, [1915] 1914–1915: Colombia.
    Sympherobius intervenalis Banks, [1915] 1914–1915:630.
italicus (Navás, 1932). See *pygmaeus* (Rambur, 1842).
killingtoni Carpenter, 1940: Western and south central United States and northern Mexico.
    Sympherobius killingtoni Carpenter, 1940:238.
    Sympherobius texanus Nakahara, 1965a:209.
klapaleki Zelený, 1963: Europe.
    Sympherobius klapaleki Zelený, 1963:59.
    Sympherobius hyalinus Monserrat, 1976a:200.
laetus Steinmann, 1967. See *pygmaeus* (Rambur, 1842).
lambereti Navás, 1910. See *pygmaeus* (Rambur, 1842).
limbus Carpenter, 1940: Southwestern United States.
    Sympherobius limbus Carpenter, 1940:236.
limpida (Navás, 1909). See *fuscescens* (Wallengren, 1863).
luojiaensis Yang, 1980: China.
    Sympherobius luojiaensis Yang, 1980:90, 92.
maculipennis Kimmins, 1929: Southern South America.
    Sympherobius maculipennis Kimmins, 1929:189.
manchuricus Nakahara, 1960: Manchuria.
    Sympherobius manchuricus Nakahara, 1960:18.
marginatus (Kimmins, 1928): Guatemala, Mexico.
    Sympheromima marginata Kimmins, 1928:363. New Combination.
marmoratipennis (Blanchard in Gay, 1851): Southern South America.
    Megalomus marmoratipennis Blanchard in Gay, 1851:127.
marshami (Stephens, 1836). See *elegans* (Stephens, 1836).
matsucocciphagus Yang, 1980: China.
    Sympherobius matsucocciphagus Yang, 1980:88, 92.
melanogaster Navás, 1915: Spain.
    Sympherobius melanogaster Navás, 1915b:250 Nomen Dubium.
menendezi Navás, 1913. See *pygmaeus* (Rambur, 1842).
miranda (Navás, 1920): Argentina.
    Niremberge miranda Navás, 1920:62.
    Sympherobius molinarii Nakahara, 1960:21.
molinarii Nakahara, 1960. See *miranda* (Navás, 1920).
nigricornis Tjeder, 1961. See *smithersi* Nakahara,1960.
notatus Kimmins, 1932: West Indies (St. Vincent Island).
    Sympherobius notatus Kimmins, 1932:160.
occidentalis (Fitch, [1855] 1854): Eastern United States.
    Hemerobius occidentalis Fitch, [1855] 1854:799.
okinawensis Kuwayama, 1964. See *tessellatus* Nakahara, 1915.
outereloi Monserrat, 1976: Spain.
    Sympherobius outereloi Monserrat, 1976b:16.
parvulus (Rambur, 1842): Canary Islands.
    Mucropalpus parvulus Rambur, 1842:422 Nomen Dubium (=*Sympherobius pygmaeus* ?).
parvus (Krüger, 1922): Unknown.
    Spadobius parvus Krüger, 1922:171 Nomen Nudum.
paucinervis (Zetterstedt, 1840). See *elegans* (Stephens, 1836).

pellucidus (Walker, 1853): Europe.
   Hemerobius pellucidus Walker, 1853:284.
   Sympherobius carpathicus Kis, 1965:103.
perparvus (McLachlan, 1869): Central and western United States and northern Mexico.
   Hemerobius perparvus McLachlan, 1869:22.
   Sympherobius sparsus Banks, 1911:346.
pictus (Banks, 1904): Southwestern United States and northern Mexico.
   Hemerobius pictus Banks, 1904c:62.
pumilio (Stein, 1863). See *pygmaeus* (Rambur, 1842).
pupillus Navás, 1915: Mexico.
   Sympherobius pupillus Navás, 1915a:151.
pygmaeus (Rambur, 1842): Europe, Asia, Middle East and northern Africa.
   Mucropalpus pygmaeus Rambur, 1842:422.
   Micromus pumilio Stein, 1863:419.
   Sympherobius conspersus Navás, 1908a:26.
   Sympherobius gratiosus Navás, 1908a:26.
   Sympherobius venosus Navás, 1908a:27.
   Sympherobius lambereti Navás, 1910a:69.
   Sympherobius bellus Navás, 1911:208.
   Sympherobius menendezi Navás, 1913:99.
   Sympherobius fortini Lacroix, 1924:116.
   Nefasitus italicus Navás, 1932:25.
   Sympherobius laetus Steinmann, 1967:156.
quadricuspis Oswald n. sp.: Arizona.
   Sympherobius quadricuspis Oswald n. sp.
riudori Navás,1915: Iberian Penninsula.
   Sympherobius riudori Navás, 1915d:50.
sanctus Tjeder, 1939. See *fallax* Navás, 1908.
schmitzi Navás,1908. see *fallax* Navás, 1908.
scriptus (Navás, 1917): Argentina.
   Coloma scriptus Navás, 1917:400.
signatus (Krüger, 1922): Unknown.
   Spadobius signatus Krüger, 1922:171 Nomen Nudum.
similis Carpenter, 1940: Arizona.
   Sympherobius similis Carpenter, 1940:236.
smitheri Nakahara, 1960. See *smithersi* Nakahara, 1960.
smithersi Nakahara, 1960: Southern Africa.
   Sympherobius smitheri Nakahara, 1960:20 (an incorrect original spelling of a patronym based
     on the surname of the Australian entomologist C. N. Smithers).
   Sympherobius smithersi Nakahara, 1960 (a justified emendation of *S. smitheri* Nakahara first
     used by Tjeder, 1961:350).
   Sympherobius brincki Tjeder, 1961:343.
   Sympherobius impar Tjeder, 1961:347.
   Sympherobius nigricornis Tjeder, 1961:341.
sparsus Banks, 1911. See *perparvus* (McLachlan, 1869).
stangei Nakahara, 1960. See *angustus* (Banks, 1904).
striatellus (Klapálek, 1905). See *elegans* (Stephens, 1836).
tenellus Navás, 1908. See *fallax* Navás, 1908.
tessellatus Nakahara, 1915: Japan.
   Sympherobius tessellatus Nakahara, 1915:22.
   Sympherobius okinawensis Kuwayama, 1964:39.

texanus Nakahara, 1965. See *killingtoni* Carpenter, 1940.
tristis Navás, 1914. See *angustus* (Banks, 1904).
umbratus (Banks, 1903): Eastern United States and Arizona.
   Hemerobius umbratus Banks, 1903:242.
   Sympherobius gracilis Carpenter, 1940:231.
venosus Navás, 1908. See *pygmaeus* (Rambur, 1842).
venustus Navás, 1908. See *elegans* (Stephens, 1836).
vicentei (Navás, 1914). See *elegans* (Stephens, 1836).
weisong Yang, 1980: China.
   Sympherobius weisong Yang, 1980:89, 92.
wuyianus Yang, 1981: China.
   Sympherobius wuyianus Yang, 1981:192, 195.
yunpinus Yang, 1986: China.
   Sympherobius yunpinus Yang, 1986:157, 164.
zelenyi Alayo, 1968: Cuba.
   Sympherobius zelenyi Alayo, 1968:21.

Note Added in Proof: In a recent biography of the 19th century American entomologist Asa Fitch, J. K. Barnes (1988, Asa Fitch and the emergence of American Entomology, New York State Museum Bulletin No. 461: viii + 1–120) has provided a comprehensive list of the 451 species described by Fitch during the mid-1800's. Remarkably, from Fitch's detailed personal collection registers, Barnes was able to compile for each species a list of specimens which were present in Fitch's collection no later than the year in which the original description of each was published. Since Fitch did not designate holotypes (Barnes, 1988:86), these lists represent for many species, including two North American species of *Sympherobius,* the closest available approximation of their syntypical series.

Barnes' (1988:105) data on the syntypes of *Sympherobius amiculus* (Fitch) and *S. occidentalis* (Fitch) are given verbatim below with added notes. These data supplement and/or modify the interpretations given in the main text of the primary types of these species. In the quotations below, Barnes' "Extant Specimens" listings include only those specimens known to reside in the collections of the New York State Museum, National Museum of Natural History, Museum of Comparative Zoology (Harvard University) and the Museum National d'Histoire Naturelle, Paris. Other specimens may be present in collections not investigated by Barnes.

    "*Sympherobius amiculus* (Fitch).

   Original Specimens: *2131, Salem, NY, 20.viii.1852, on basswood bush, Esq. Martin's meadow; **3964, Salem, NY, 30.v.1854, about the house; 9085, IL, 7.x.1854, beat from peach trees, Burnett's.

   Extant Specimens: **3964/Type 10449/*Hemerobius amiculus* (MCZ); 9085/ Fitch Collection/*Hem. amic.* var. a (UNSM)."

Notes: Since Fitch did not designate types, and since the type series of *S. amiculus* is now known to have been composed of more than one specimen, Fitch's specimen number "3964" (MCZ type #10,449) cannot now be considered a holotype, as assumed by Carpenter (1940: 229) and as stated in the main text above. This specimen must now be interpreted as a lectotype designated by Carpenter's holotype assumption (ICZN, 1985: Article 74b). Barnes' data also allows the type locality of *S. amiculus* to be stated more precisely: UNITED STATES: New York: Washington Co.: Salem.

    "*Sympherobius occidentalis* (Fitch).

   Original Specimens: 8392, IL, 2.x.1854, on ash leaves, beside Henderson River."

Note: The repository of the holotype of *S. occidentalis* remains unknown. If this specimen is still extant, the additional data provided by Barnes should facilitate its recognition.

PALLODES AUSTRINUS, A NEW SPECIES OF NITIDULIDAE (NITIDULINAE) WITH DISCUSSIONS ON *PALLODES* MYCOPHAGY

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Abstract.—*Pallodes austrinus* is described as new and illustrated. *Pallodes pallidus* is also illustrated and differences of both species are discussed. *Pallodes* adult and larval mandibles are adapted for mycophagy with cutting spines on the incisor edges, a well developed prostheca and an asperate mola. *Pallodes pallidus* has a wider mushroom host range than *P. austrinus* but with large overlap.

Pallodes species are commonly found on fresh mushrooms. Although diverse in the tropics only two species are known from North America: *Pallodes plateosus* Schaeffer in the southern Rockies of Arizona and New Mexico and *Pallodes pallidus* Beauvois in eastern temperate forests (Parsons, 1943). Parsons (1943) designated *P. pallidus* as the genotype.

During a recent survey of mycophagous Coleoptera, specimens of *P. pallidus* and a new species of *Pallodes* were collected from fresh mushrooms. Mixtures of both species were found in loaned material. Detailed examination of specimens revealed that Parsons (1943) had unknowingly described and illustrated both species as *P. pallidus.*

Lawrence (1988a) stated that most larval nitidulids have retracted mouthparts that are pushed forward by the longitudinal cardines and that the prostheca is complex. In addition, the adult nitiduline mandible is equally impressive as the larval nitiduline mandible.

The objectives of this paper are: 1) to clarify the identity of the two Eastern species of *Pallodes* including a description of the new species, and 2) to describe *Pallodes* larval and adult mouth parts. Information on mushroom hosts and seasonal abundance is also provided.

METHODS

Specimens were borrowed from the following institutions: Florida State Arthropod Collections (FSAC), North Carolina State University Entomology collection (NCEC) and the National Museum of Natural History (USNM). Additional specimens were supplied by Karl Stephan (KSC). Paratypes were sent to the above and to the British Museum (Natural History) (BMNH), Canadian National Collection (CNC), Museum de'Histoire naturelle, Geneva (MHNG), Ohio State University Collection (OSUC), and the Snow Entomological Museum, University of Kansas (SEM). Each museum received 5 paratypes (2 male, 3 female). The holotype and allotype were deposited in the University of Arkansas Insect Collection (UAIC). Remaining paratypes are retained in the R. A. B. Leschen collection (RLC) and KSC.

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Several specimens of each *Pallodes* species were dissected in glycerin after being soaked in hot 10% KOH. Body parts and limbs were slide mounted in CMC-AF medium or prepared for scanning electron microscopy. Disarticulated specimens were stored in genitalia vials and pinned.

Terms for male genitalia follow Sharp and Muir (1912) and those for the female ovipositor follow Parsons (1943). Homologies are not attempted for genitalia.

Pallodes austrinus, new species

Description. Male. Length 3–4 mm. Color testaceus. Strongly convex and glabrous. Fine microsculpture over entire body, appearing iridescent under high magnification. Terminal article of labial palp with 2 ventro-lateral rows of pedicellate setae set in longitudinal crypts (Figs. 2E, 3C). Third antennomere one-third longer than the fourth, fourth equal to the fifth (Fig. 1G). Pronotal margin broadly lobate medially. Elytron with 9 punctate stria confused in apical fourth. Coxal lines of abdominal sternite I shallow and reaching the middle of the segment (Fig. 1I). Protibial fossorial spines separated by at least one and a half times their basal width (Fig. 1A). Mesotibia with anterior spinous row separated from tibial angle by the length of a single spine (Fig. 1C). Metatarsi with basal tarsomere about one third length of metatibia (Fig. 1F). Aedeagus with setal fans of tegmen lobe confined laterally; median strut and basal piece strongly developed (Fig. 2A). Other characters as described for the genus by Parsons (1943).

Female. Same as male. Ovipositor with minutely serrate lateral edges at apical third and first and second valvulae strongly separated ventrally (Fig. 2C).

Holotype. Male, USA, AR, Logan Co., Cove Lake, 9 mi. SW of Paris, 3 June 1986, Ex *Russula*, R. A. B. Leschen (UAIC).

Allotype. USA, AR, Cross Co., Village Cr. St. Park, Augell Trail, Ex *Lactarius piperatus*, R. A. B. Leschen.

Paratypes. Arkansas: Washington Co., L. Wedington 12 mi. W. of Fayetteville, R. A. B. Leschen: 13 July 1986, Ex gilled fungus (1), 8 June 1986, Ex gilled fungus (1), 25 May 1986, Ex *Russula* (19); 25 May 1986, *Laccaria laccata* (2); 25 May 1986, Ex *Amanita* (1); 8 June 1986, Ex *Lactarius* (3); 8 June 1986, Trichalomataceae (1); 8 June 1986, Ex *Amanita* (1); 8 June 1986, Ex *Russula* (28); 8 June 1986; Ex *Amanita rubescens* (16); Logan Co., Mt. Magazine, Brown Springs, R. A. B. Leschen: 1 July 1986, Ex *Boletus* (1); 18 August 1986, Ex *Boletus* (1); 3 June 1986, Ex *Russula* (3); Logan Co., Cove Lake, R. A. B. Leschen: 3 June 1986, Ex *Russula* (6); 19 August 1986, Ex *Boletus* (1); 2 July 1986, Ex *Lactarius* (1); 28 May 1986, Ex *Russula tetans* group (1); 28 May 1986, Ex *Amanita pantherina* var. *velatipes* (6); Logan Co., 23 mi. SW of Paris off HWY 309 on National Forest Maintained Rd., 23 June 1986, Ex *Amanita rubescens,* R. A. B. Leschen (7); 17 August 1986, Ex *Amanita spreta* R. A. B. Leschen: Logan Co., Mt. Magazine, Signal Hill Trail, 1 July 1986, Ex *Boletus,* R. A. B. Leschen; Oklahoma, Latimer Co., 5 mi. SW of Red Oak, K. Stephan: 7-V-77(5); 11-1x-77(2); 11-VI-77(2); 21-VIII-77(1); Oct. 1980 (1), Aug. 1986(3); V-1983(8); VI-1983(2); VI-1984(6); IX-1984(2); V-1985(12); VII-1987(1); VI-1987(3); X-1987(3); VI-1986(6); V-1986(9); V-1987(3); IX-1986(4); X-1986(1); I-1986(1); X-1983(1); VI-1985(2); IX-1985(1); Tenn., Grundy Co., Savage Gulf St. Nat. Area, 5 mi. E of Bersheeba Spgs., 21 July 1986; Ex *Amanita,* R. A. B. Leschen (2).

Remarks. In the family treatment of Nitidulidae, Parsons (1943) did not recognize
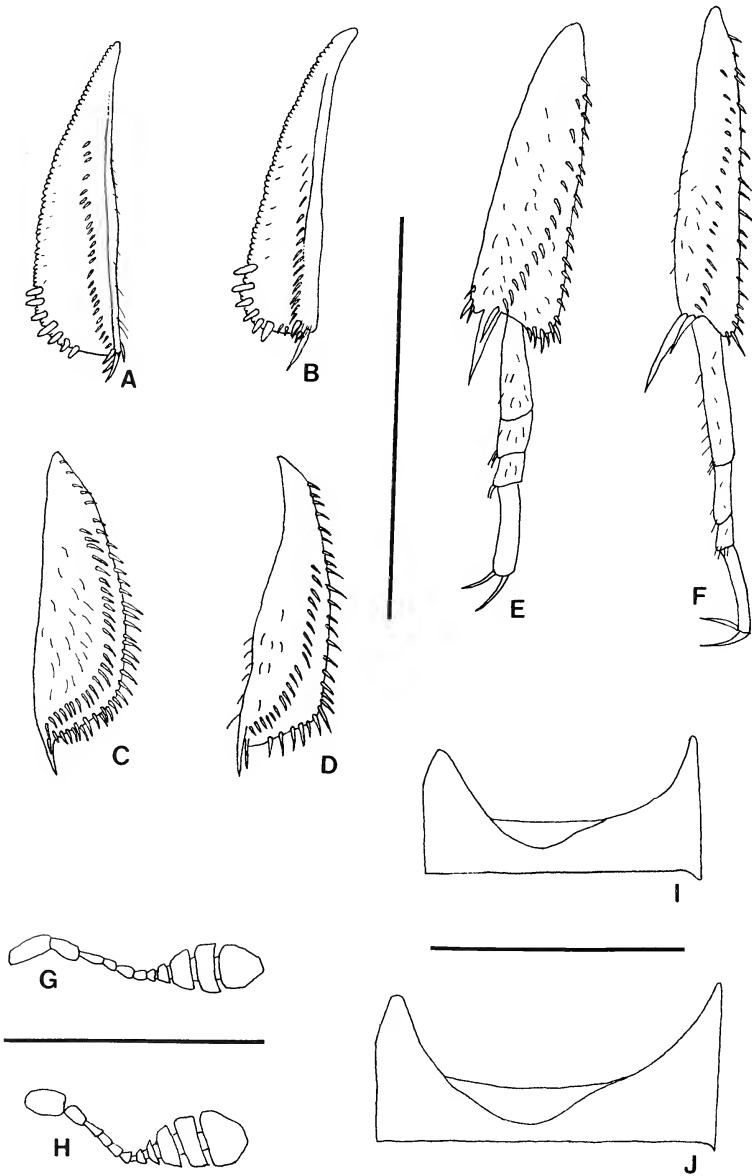
Fig. 1. *Pallodes* adult characters. A, B. Protibia, posterior aspect: A. *P. austrinus*. B. *P. pallidus*. C, D. Mesotibia, anterior aspect: C. *P. austrinus*. D. *P. pallidus*. E, F. Metatibia and metatarsa, anterior aspect: E. *P. austrinus*. F. *P. pallidus*. G, H. Antenna, ventral aspect: G. *P. austrinus*. H. *P. pallidus*. I, J. Coxal lines on right half of first abdominal ventrite. I. *P. austrinus*. J. *P. pallidus*. (Scale bar = 1 mm.)
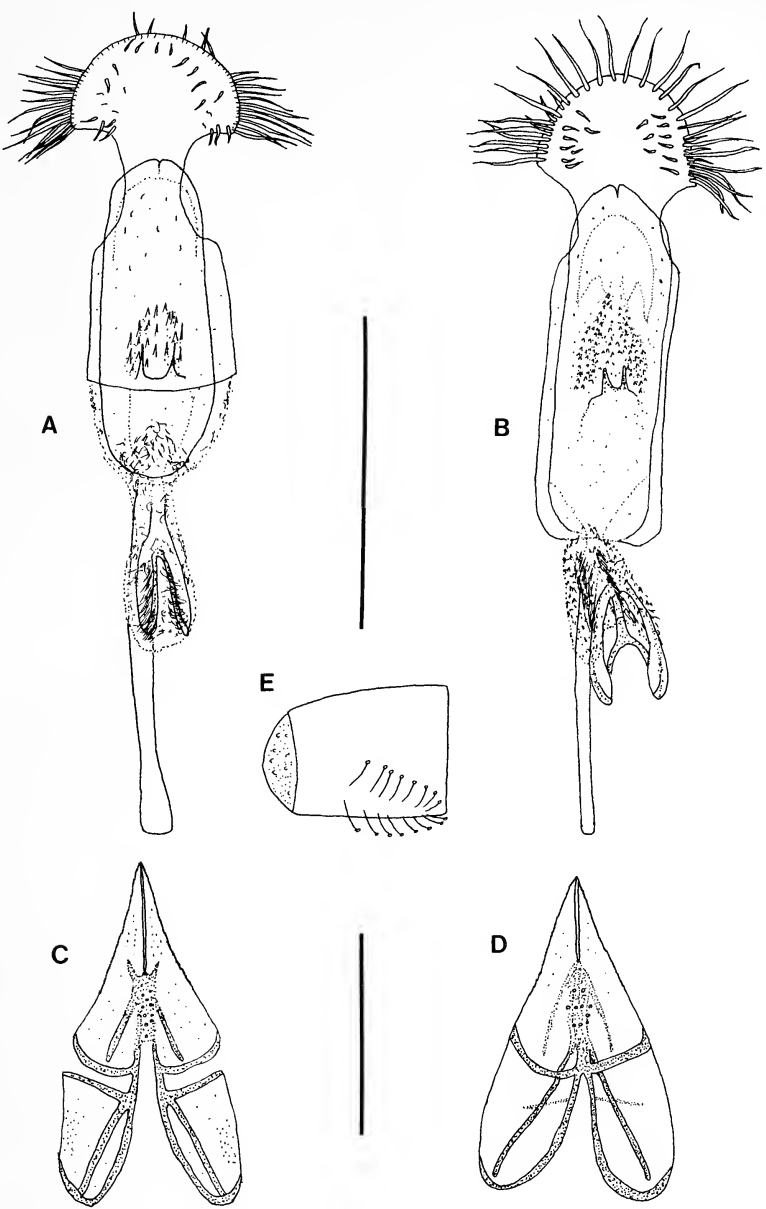
Fig. 2. Genitalia of *Pallodes*. A, B. Aedeagus: A. *P. austrinus*. B. *P. pallidus*. C, D. Ovipositer: C. *P. austrinus*. D. *P. pallidus*. E. *P. austrinus* labial palp, ventro-lateral aspect showing pedicellate sensilla. (Scale bar = 0.5 mm.)

one of the two sympatric species of *Pallodes*. He illustrated *P. pallidus* with the antenna and ovipositor of *P. pallidus,* but the aedeagus of *P. austrinus.* The mouthparts illustrated by Parsons may be of either species. *Pallodes austrinus* cannot be confused with the dorso-ventrally compressed *P. pallidus* because of its convex body form. Additionally, the more compacted funnicle antennomeres (Fig. 1G, H), the pronotal margin with posterior lobe, shallow coxal lines (Fig. 1I, J) and more compacted metatarsi will easily distinguish *P. austrinus* from *P. pallidus.* Tibial chaetotaxy (Fig. 1A–F) may also be used to distinguish *P. austrinus* from *P. pallidus.*

Both species of *Pallodes* have microsculpture but *P. pallidus* is iridescent at low magnification and *P. austrinus* is iridescent only at high magnification. Most specimens of each *Pallodes* are testaceous but may have dark elytra. Only *P. pallidus* has a large dark pronotal macula coincident with dark elytra. Variation in the depth of elytral punctate stria and spacing and number of tibial spines and setae occurs for both species of *Pallodes.*

Sexes may be determined by the eighth abdominal tergite of males. The aedeagus of *P. austrinus* has setae confined to lateral areas of the tegmen lobe and a well-developed median strut (Fig. 2A); whereas, the aedeagus of *P. pallidus* has setae along entire margin of the tegmen lobe and a thin median strut (Fig. 2B). Caution should be used when dissecting *P. pallidus* males because the fragile median strut is easily broken. The ovipositor of *P. austrinus* has the first and second valvulae separated (Fig. 2C) which is unlike most *P. pallidus* that have fused first and second valvulae (Fig. 2D). The ovipositor of one specimen of *P. pallidus* was separated although all other characters were consistent.

Distribution. Arkansas, Florida, Indiana, Louisiana, North Carolina, Oklahoma, South Carolina and Tennessee.

Etymology. Austrinus, Latin for south.

PALLODES MYCOPHAGY

Adult mouthparts. The mandible of *Pallodes* adults was illustrated by Parsons (1943). The bifid apex on the incisor process bears ventral and dorsal oblique cutting spines. The incisor process is perpendicular to the mandible proper (Fig. 3A). The outer mesal edge of the mandible is smooth with only a few short spines. The prostheca is set with large spines that are folded ventrally. Lateral and proximally entad to the prostheca is an area defined by brush-lined cavities. Just posterior to the prostheca is a well developed mola with ridges of posteriorly angled asperities. At the base of the mandible and surrounding the mola basally and laterally is a large brush. The food meatus is boarded ventrally by the maxilla with brushes and spines on the apical and inner lateral margins of the lacinea.

Larval mouthparts. The larval mandible was illustrated by Böving and Rozen (1962). The incisor process is scoop-shaped and somewhat laterally compressed, with peripheral oblique cutting spines (Fig. 3B). The well-developed prostheca is bound dorsally by a field of brushes and ventrally with minute rows of asperities. The base of the mandible consists of a large mola that has an expansive field of fine ridges of asperities dorsally and a spinous inner mesal margin that is continuous ventrally. The labial palpus has an apical brush with accessory spines. The hypopharyngeal sclerome is heavily sclerotized and the epipharynx is well-developed with posteriorly directed setae.

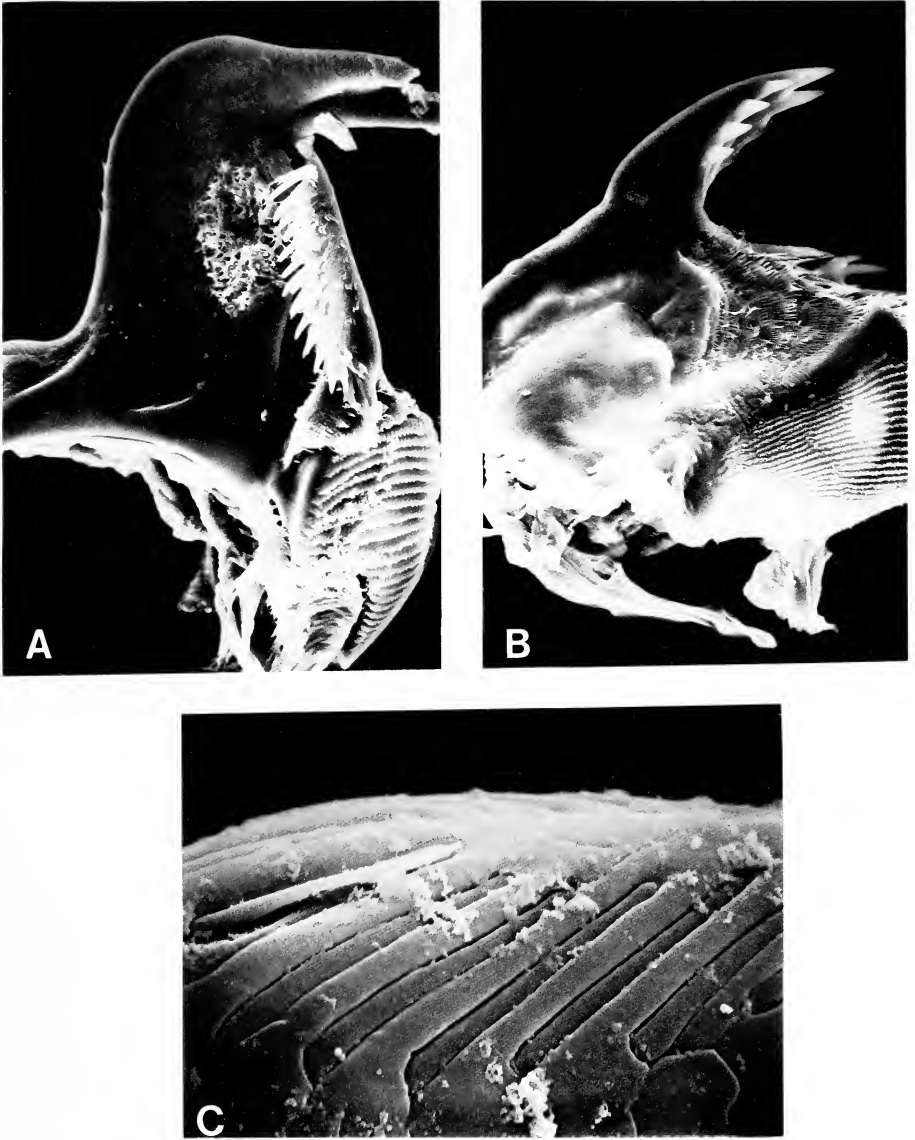Larvae and adults bear slicing teeth on incisor surfaces, prosthecae for tearing,

Fig. 3. Mouthparts of *Pallodes*. A. SEM micrograph of *Pallodes* adult mandible, ventral aspect. B. SEM micrograph of *Pallodes* larval mandible, dorsal view. C. SEM micrograph showing reception of pedicellate sensillae into crypts on the labial palp.

molae for grinding and compression and brushes for manipulation of the bolus. Obliquely set slicing teeth are found on various mushroom feeders (Lawrence, 1988b). Prosthecae are well developed in *Pallodes* larvae (like most Nitidulinae) and modified in the adults. The folded appearance of the adult prostheca is oriented in the same vertical plane as the cutting teeth on the bifid apex of the incisor process. The mola

may act as a press for compaction or grinding of the bolus. In the larva the mola extends onto the ventral face of the lower mandible and it may act against the hypopharyngeal sclerome. The dorsal areas of the larval mandible may act with the epipharynx to sieve excess water naturally occurring in mushroom tissue. The adult mola seems to compress the bolus vertically whereas the larva bolus is compressed horizontally.

Pallodes austrinus and *P. pallidus* have broad mushroom host ranges. *Pallodes austrinus* has a narrower host breeding range and reproduction has been confirmed on *Amanita, Boletus, Lactarius* and *Russula* whereas *P. pallidus* has been reared from *Amanita, Boletus, Laccaria, Lactarius, Pluteus, Russula* and *Strobilomyces*. Host ranges overlap and *P. austrinus* is excluded from many mushroom families that serve as hosts for *P. pallidus. Pallodes pallidus* was found most frequently on Trichalomataceae. *Pallodes austrinus* was found mostly on Russulaceae. Host patterns are similar to Ashe's (1984) pattern 1 for gyrophaenine staphylinids. A more defined host pattern may develop for *Pallodes* with the addition of future data. Host records prior to this study may be unreliable since the two species were confused.

Pallodes shows a bimodal seasonal abundance with peaks corresponding to major flushes of mushrooms and high mean monthly rainfall. *Pallodes austrinus* was most common during the months of June, August and September and *P. pallidus* was most common during the months of May, June and September. Based on rearing data and presence of teneral adults, *P. austrinus* generally reproduces in spring and early summer, and *P. pallidus* reproduces from May to September.

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A NEW SPECIES OF *PULICELLA* FROM TANZANIA WITH COMMENTS ON THE GENUS (SIPHONAPTERA: PULICIDAE)

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Abstract.—A new species of *Pulicella* collected on *Otomys angoniensis* in the Ngorongoro Crater of Tanzania is described. Its affinities with the only other species in the genus are discussed.

During a recent comparative study of the sexual apparatus in the males of the pulicoid genera by one of us (TBC), large numbers of specimens were borrowed from various persons and institutions. Among the specimens received from the British Museum (Natural History) was a single male collected in the Ngorongoro Center, Tanzania, by the late C. A. Hubbard. Although identified as *Xenopsylla raybouldi* Hubbard, 1963, it was immediately obvious that it was not this species and probably did not belong to this genus. Accordingly it was labeled genus X in the dissertation (Cheetham, 1987) in the expectation that it would subsequently be described as a new taxon. On the basis of phallic characters the specimen belongs to the Xenopsyllini, but is nearer to *Pariodontis* and *Procaviopsylla* than to other genera belonging in this tribe. Although it does not fit in any genus where males are known, comparison with the generic diagnosis of *Pulicella* Smit, 1964, in which the male is unknown, strongly suggests that it may be an undescribed species belonging to this genus. However, there is some variance in characters between those described by Smit and those found in the specimen under discussion. Following are the main attributes shared by both specimens: a) frontal tubercle absent; b) trabecula centralis present; c) midcoxa with complete sulcus; d) lowest abdominal tergal leucodiscs located obliquely above and in front of the spiracle; e) spiracular fossa of tergites II–VII oval, not circular; f) spiracular fossa of tergite VIII sickle-shaped; g) all fifth tarsal segments with 4 pairs of evenly spaced lateral plantar setae.

The genus *Pulicella* was erected for a single specimen collected in the Misuku Hills (ca. 33°30′E, 09°40′S) in northern Malawi, from *Rattus delectorum.* The generic diagnosis is thus based on some characters that may vary with sex. Accordingly, our specimen is described as a new species of *Pulicella,* although there are indications that it may constitute a new genus in the Xenopsyllini.

Pulicella aenigma, new species
### Figs. 1–7

Diagnosis. Similar to the genera *Pariodontis* and *Procaviopsylla* in the anatomy of the genitalia. Differing from the former in lacking the acute genal lobe, the false comb on the hind coxa, and stout bristles on the thorax and abdomen. From the latter, it differs in lacking the pyriform hind coxa and its apical false comb. In addition, the antennal clava in *Procaviopsylla* species is conspicuously segmented throughout its
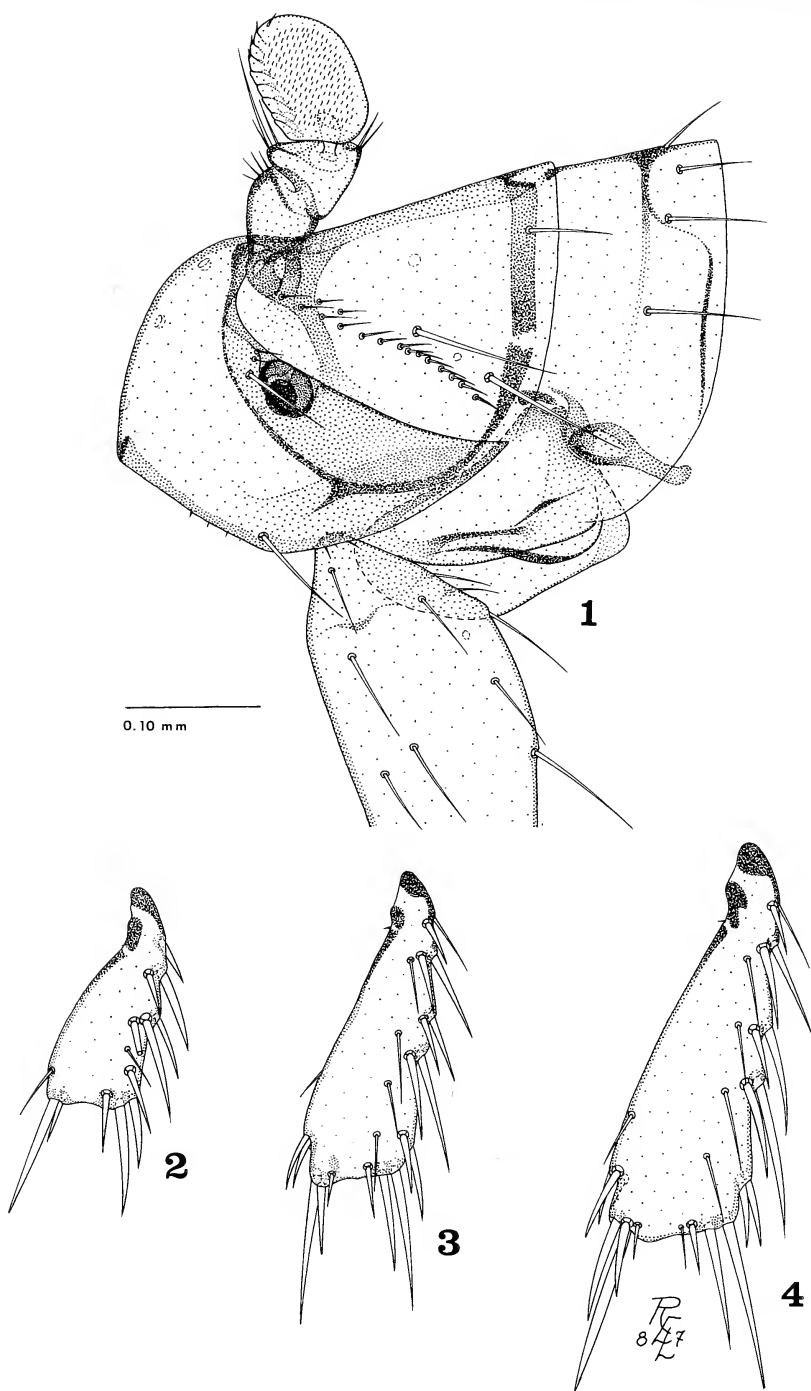
Figs. 1–4. *Pulicella aenigma* holotype male. 1. Head and prothorax. 2. Foretibia. 3. Midtibia. 4. Hindtibia.

length, whereas segmentation is only barely visible along the dorsal margin in this taxon. It differs from the only known specimen of *Pulicella,* a female, in the following characters: a) ventral margin of gena lacking pronounced lobe; b) trabecula centralis smaller than eye; c) eye well developed and with a trace of an internal sinus (left eye cracked); d) second midtarsal segment longer than first; e) tibial chaetotaxy dissimilar; f) 3 preapical plantar setae, not 2; g) much smaller, lighter, and less setose.

Description. Head (Fig. 1). Preantennal portion of head blunt, lacking frontal tubercle and conspicuous lobe on ventral margin. Ocular seta situated in front of well-developed eye. With a single seta on genal margin. Trabecula centralis circular, smaller than eyes and situated between them. Antennae as illustrated, with clava showing only slight evidence of segmentation along dorsal margin. Antennal fossa deep, enclosed ventrally by genal process and bordered dorsally by a row of 15 fine bristles, above which is 1 minute and 1 long bristle. Occipital row consisting of 1 long ventral seta and 2 much smaller setae dorsally per side. Labial palpi 5-segmented, extending to apex of forecoxa, or perhaps to middle of trochanter. Thorax. Pronotum and metanotum of equal length, mesonotum about 1½ times as long as pronotum. Pronotum with 4–5 long setae per side. Mesonotum with 4 long setae per side and 1 long seta per side on mesepimeron. Metanotum with 4 long setae per side, metepisternum with 3 long bristles, and metepimeron with 4 long bristles arranged in a curved row. Legs. Forecoxa as shown in Figure 1, sparsely clad with long setae. Forefemur with 4–5 fine, submarginal setae on outer surface. Foretibia as in Figure 2. Foretarsal segments 1 through 4 only slightly subequal, almost moniliform. Foretarsal segment 5 with 4 pairs of lateral plantar bristles with pair number 3 slightly shifted onto plantar surface, with 1 long and 2 short preapical plantar bristles and 5–6 minute plantar setae as shown in Figure 6. Midcoxa with a complete oblique sulcus and lacking setae on inner surface. Midfemur with a few fine setae on inner surface. Midtibia as shown in Figure 3. Midtarsal segments 1 and 3 of approximately equal length, segment 2 almost 1½× as long as adjacent segments, segment 4 hardly longer than wide, segment 5 as described for foretarsus. Hindcoxa somewhat intermediate between *Procaviopsylla* and *Xenopsylla,* lacking apical false comb and with 2 subspiniform bristles on inner surface near anterior margin as illustrated in Figure 7. Hindfemur with 5–6 fine setae arranged in a row on inner surface and 2 subapical, submarginal bristles on outer surface. Hindtibia as shown in Figure 4. Hind tarsal segment 4 about as long as wide, segment 3 about twice as long as 4, 2 about twice as long as 3, and 1 about twice as long as 2. Hind tarsal segment 5 as described for foretarsus. Abdomen. Tergite I with an anterior row of 6, a median row of 4, and a posterior row of 6 long setae. Spiracular fossa ovate-cordiform. Tergites II–VI with 4 or 5 bristles per side arranged in a single row. Tergum VII with 9 long bristles; 3 longer bristles each side and 3 shorter dorsal bristles that arise near the margin, between the 2 antepygidial bristles. The latter, 1 per side, arise on a marginal pedestal and are flattened and contorted as shown in Figure 5. Lowest tergal leucodiscs situated obliquely dorso-cephalad of the spiracular fossa on segments III–VII. Spiracular fossa of tergum VIII sickle-shaped. Sternites III–VII with 2 long setae per side. Sternum VIII with 3 long setae per side. Periphallic Structures. Apodeme of tergum IX elongate, triangular in lateral view. Manubrium long, thin and rod-like, not broadly fused with apodeme. P1 and P2 slightly subequal in length, with P1 more than 5.5 times as long as broad. P2 slightly broader than P1, with a short apodeme. P3 triangular,
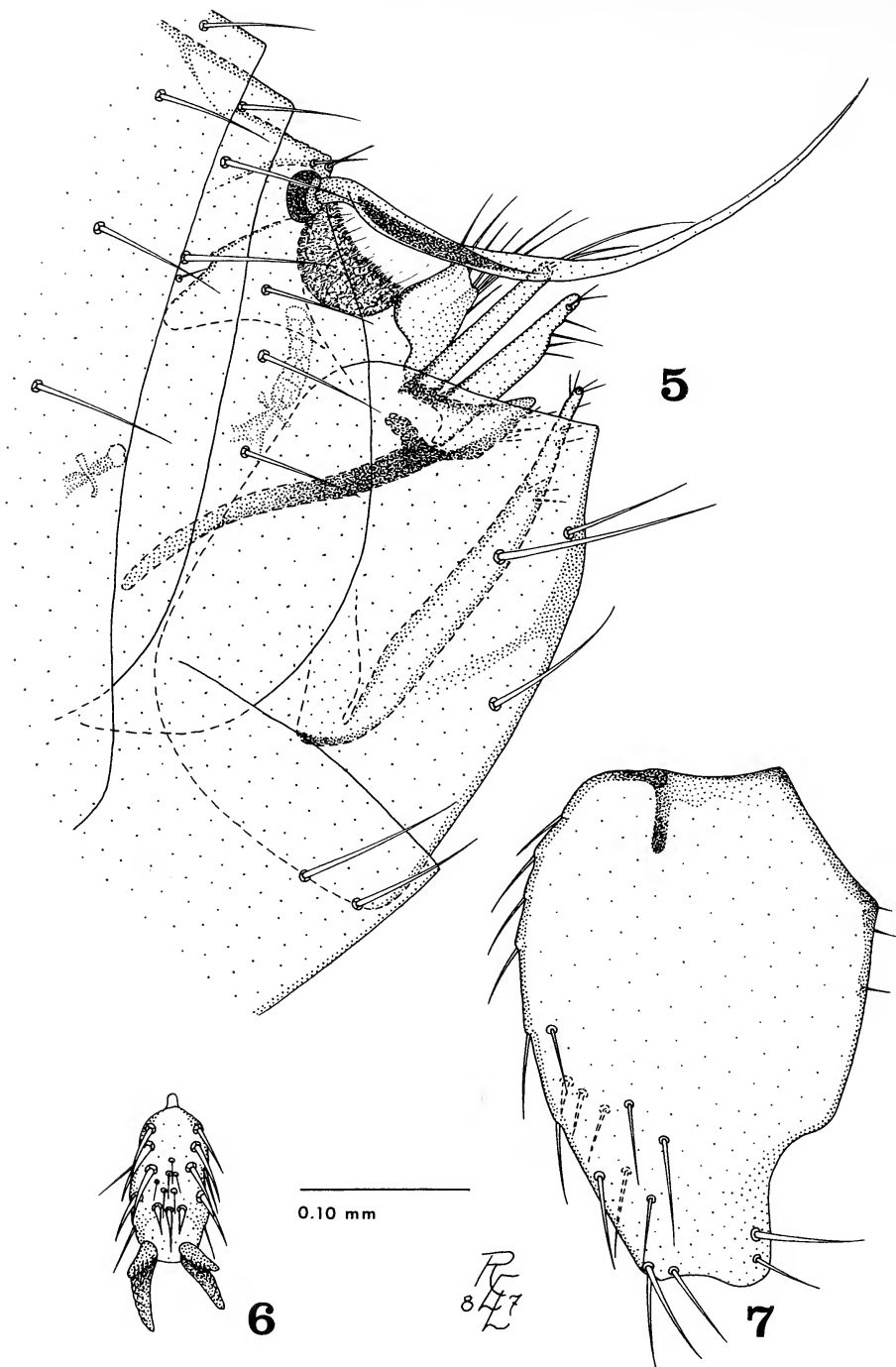
Figs. 5–7. *Pulicella aenigma* holotype male. 5. Modified abdominal segments. 6. Foretarsus. 7. Hindcoxa.

large, broadly fused with base of manubrium and bearing a single, tooth-like lateral projection and a fringe of 5 fine setae along caudal margin. Distal arm of sternum IX long, broad basally, tapering distally. Phallosome. Aedeagal apodeme 10 times as long as broad, 3 times as long as aedeagus, constricted basally, smoothly tapering and upturned apically, terminating in a filiform projection. Ventral margin of median lamina strong, lateral laminae hyaline. Penis rods curving 360 degrees over apodeme. Apodemal rod well developed. Lateral fulcral lobes evidently fused with lateral laminae; thin and broadly curved. Median dorsal lobe with strong, curved dorsal margin. Suspensory sclerites absent. Inner tube large, expanded proximally with a dorsal dome; strong walls over proximal ⅔; proximal projections prominent, smoothly tapering overall. Vesicle large, with strong margins. Ribs developing laterally into small pads lying dorsad of lateral fulcral lobes. Sheath tapered distally and pointed at dorsal apex. Lateral lobes indistinct, with wings not clearly discernible and accessory lobes seemingly absent.

Etymology. The specific epithet is Latin for something difficult to understand or explain and alludes to the fact that only this single specimen has been collected from one of the prime scenic attractions in eastern Africa.

Holotype. Male from Ngorongoro Crater floor, 5,000 ft (1,524 m), Tanzania, from *Otomys angoniensis,* 20.I.1963, *leg.* C. A. Hubbard. Returned to the British Museum (Natural History) collection of fleas at London, England.

Remarks. That the genus was erected with a female as holotype allows for speculation as to how many of the characters by which this taxon differs from *Pulicella macrotheca* are of a sexual nature. Smit (1964) gives 3.5 mm as the overall length of *P. macrotheca.* The overall length of *P. aenigma* is 1.4 mm. Such measurements are usually viewed as relatively inconsequential because the degree of abdominal expansion or contraction may vary considerably, depending upon how the specimen was processed before study. It is also recognized that male fleas tend to be smaller than the females, sometimes spectacularly so. Further, in long series of fleas, it is not uncommon for the measurements of the smallest female to overlap those of the largest male. The inescapable conclusion is that size is not a valid taxonomic character in this group.

Smit (1964) also remarks on the heavy pigmentation of his specimen, stating that, after 5 days in 10% KOH, his specimen was still very dark. Such is certainly not the case with our male. Again, pigmentation is not a taxonomic character of much value in fleas, but seldom is there great variation among the species belonging to the same genus.

Of perhaps more immediate importance is a consideration of the differences between this specimen, as set down in the diagnosis, and *P. macrotheca,* as described by Smit (1964). First, although there is no pronounced lobe on the ventral margin of the gena in the male, there is an incipient lobe present that may be somewhat deemphasized because of the totally different configuration of the head.

With respect to the trabecula centralis, there seems to be some confusion surrounding the applications of this term. The glossary to volume V of Hopkins and Rothschild (1971) lists three other names for this structure, all of which are treated as synonyms of each other. These are "area communis," "central tuber," and "tuber centralis." The latter two are obviously English and Latin versions of the same thing. By strict definition all four of these terms refer to the ". . . pale ovoid area where the

walls of the antennal fossae of the two sides are fused together to form an incipient central tuber . . ." (Hopkins and Rothschild, 1971). This definition is misleading in a number of ways. As often as not, the area communis, which seems to be the preferred term, is circular and dark, not pale and ovoid. That it forms an "incipient central tuber" is redundant because the latter is a synonym of the former. The matter is further confused by Smit's statement that a trabecula centralis is a diagnostic character for *Pulicella* and that ". . . of all genera of Pulicidae . . . this trabecula is only present in *Pariodontis,* while *Procaviopsylla* and *Xenopsylla* have an area communis." Smit's figure 6 shows this as a darkened area behind and slightly below the eye, which he indicates is small and globular and lacking an internal sinus. In our male, the area communis is circular, dark in color, and situated in the area between the well developed, ovoid eyes. Its position is certainly dictated by the configuration of the head and the trough-like antennal fossae.

The differences in leg segment proportions and chaetotaxy are difficult to explain. Although legs in the order vary from group to group, from deciduous in some tungids to massive in malacopsyllids, their development and chaetotaxy tend to be quite similar between the sexes in all the genera with which we are familiar.

These considerations aside, it is evident that the solution to the questions aroused by the discovery of this species must await further collections from central and eastern Africa.

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A NEW SPECIES OF *PLOCOPSYLLA* JORDAN, 1931 (SIPHONAPTERA: STEPHANOCIRCIDAE) FROM ARGENTINA

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Abstract.—A new species of *Plocopsylla* Jordan, 1931 (Siphonaptera: Stephanocircidae) from Argentina is described. The holotype female and two paratype females of this new taxon were assigned originally to *Plocopsylla chiris* Jordan, 1931b. Because of dimorphism between these females and the male lectotype of *P. chiris* and host specificity data involving the genus *Plocopsylla,* these three females are described as new. The identifications of two other females previously assigned to *P. chiris* are discussed.

The family Stephanocircidae includes the Australian subfamily Stephanocircinae and the Central and South American subfamily Craneopsyllinae. The former contains two genera that are characterized by having well-developed helmet sutures. The latter contains seven genera, *Plocopsylla* among them, that have helmet sutures that are either vestigial or that merge with the interantennal suture. *Plocopsylla* is most similar to *Craneopsylla* Rothschild, 1911, and *Sphinctopsylla* Jordan, 1931, but it differs in several characters, including the fact that both genal bristles arise anterior to the cibarial pump. Males of *Plocopsylla* can be readily identified by the contours of the ninth sternite, the movable process, and the clasper with its mesal process, all of which are species-specific. Females lack such definite characters, and there are several instances in which the females of one species strongly resemble those of another.

It is not too unexpected that, with one possible exception, all females identified as *P. chiris* are not that species. Sexual dimorphism is unknown in any of the 18 species of *Plocopsylla* in which both sexes are known. Yet, in revision of the genus (Schramm, 1987), it was noted that morphological differences existed between the lectotype male and paralectotype female of *P. chiris*. In the lectotype, the anterior-to-posterior prectenidial helmet width is noticeably less than the length of the longest helmet spine. This specimen also has helmet spines with prominent V-shaped basal notches, a genal spine that is separated from the adjacent spine in the genal comb by a gap roughly ½ the basal width of the genal spine, and a 3-2-2-3-3-3-4 bristle arrangement along the posterior margin of the hind tibia. In contrast, the female initially designated the paralectotype of *P. chiris* and the other members of the type material of our new species have an anterior to posterior prectenidial helmet width that is slightly longer than the length of the longest helmet spine, the helmet spines lack basal notches, the genal spine is separated from the adjacent spine in the genal comb by a gap roughly equal to the basal width of the genal spine, and there is a 3-2-3-4-4-4-4 bristle arrangement on the hind tibia.

Also, it cannot be assumed that the specimens originally designated as the lectotype and paralectotype of *P. chiris* are the same species merely because they were collected from the same host. Host data for *Plocopsylla* species are incomplete but indicate

that it is not unusual to collect two, or possibly three, species belonging to this genus from a given locality, or from even the same host.

The females previously identified as *P. chiris* are assigned here to either *P. lewisi* Beaucournu and Gallardo, 1988, or to a new species. Females of these two species strongly resemble each other, but differ in the arrangement of bristles along the posterior margin of tergite VIII and in the shape of the anal stylet. The senior author examined the four females that were initially determined to be *P. chiris*. Three of these constitute the type material of the new species. Identification of the fourth, as well as of an additional female originally designated as *Craneopsylla wolffsohni* (Jordan and Rothschild, 1914), is discussed subsequently.

Plocopsylla kasogonaga, new species
Figs. 1–2, 4

Diagnosis. Females of this species strongly resemble those of *P. lewisi*. Males are unknown. Females of both species share the following characters: a) helmet spines not basally notched; b) five spines in the genal comb with the genal spine only slightly shorter than the others; c) a 3-2-3-4-4-4-4 bristle arrangement along the posterior margin of the hind tibia; and d) a spermatheca that has deep penetration of the hilla into an elongate bulga. Females of *P. kasogonaga* can be distinguished by having several long bristles below the single prominent lobe on the posterior margin of tergite VIII as shown in Figure 2 and by having an anal stylet that tapers abruptly. In contrast, females of *P. lewisi* have several long bristles arising from the smaller, more ventral of the two lobes along the posterior margin of tergum VIII as shown in Figure 3 and by having an anal stylet that tapers more gradually.

Description. HEAD (Fig. 1). Anterior to posterior prectenidial width of helmet slightly longer than length of longest helmet spine. Helmet striations with anterior ends frequently forming groups of three or four, but without actually anastomosing. With 12 helmet spines lacking V-shaped basal notches. Anterior margin of gena blunt, convex, and aligned with 8 to 15 submarginal bristles. With 5 to 8 smaller, lateral bristles located between 2 long genal bristles. Genal comb contains 5 spines, with tapered genal spine slightly shorter than length of adjacent spine in comb, and separated from adjacent spine by a gap similar to basal width of genal spine. Genal lobe truncate, with slight distal expansion. Preoral tuber with dorsal margin strongly convex, with height roughly $1.5\times$ the length. Antennal bristles arising along convex distal margin of second antennal segment, with longest bristles extending beyond apex of clava. THORAX. Pronotum with 2 rows of bristles, anterior row of intermediate-length bristles, posterior row of alternating long bristles and intercalaries. Pronotal comb with 20–24 elongate spines, with small lobe below ventralmost spine that is, at most, ½ length of adjacent spine. Mesonotum and metanotum with 3 and 2 rows of bristles, respectively, with anterior row(s) of intermediate-length bristles, posterior row of alternating long bristles and intercalaries. Mesonotum with 6 to 10 small bristles along anterior margin, frequently overlapped by pronotal comb. With two mesonotal pseudosetae per side. LEGS. Bristles along posterior margin of hind tibia with the following arrangement: 3-2-3-4-4-4-4. Lateral surface of hind tibia with variable bristle arrangement. ABDOMEN. Tergites each with 2 rows of bristles, similar to those of pronotum. Marginal spinelets of anterior tergites as follows: I 4/3-
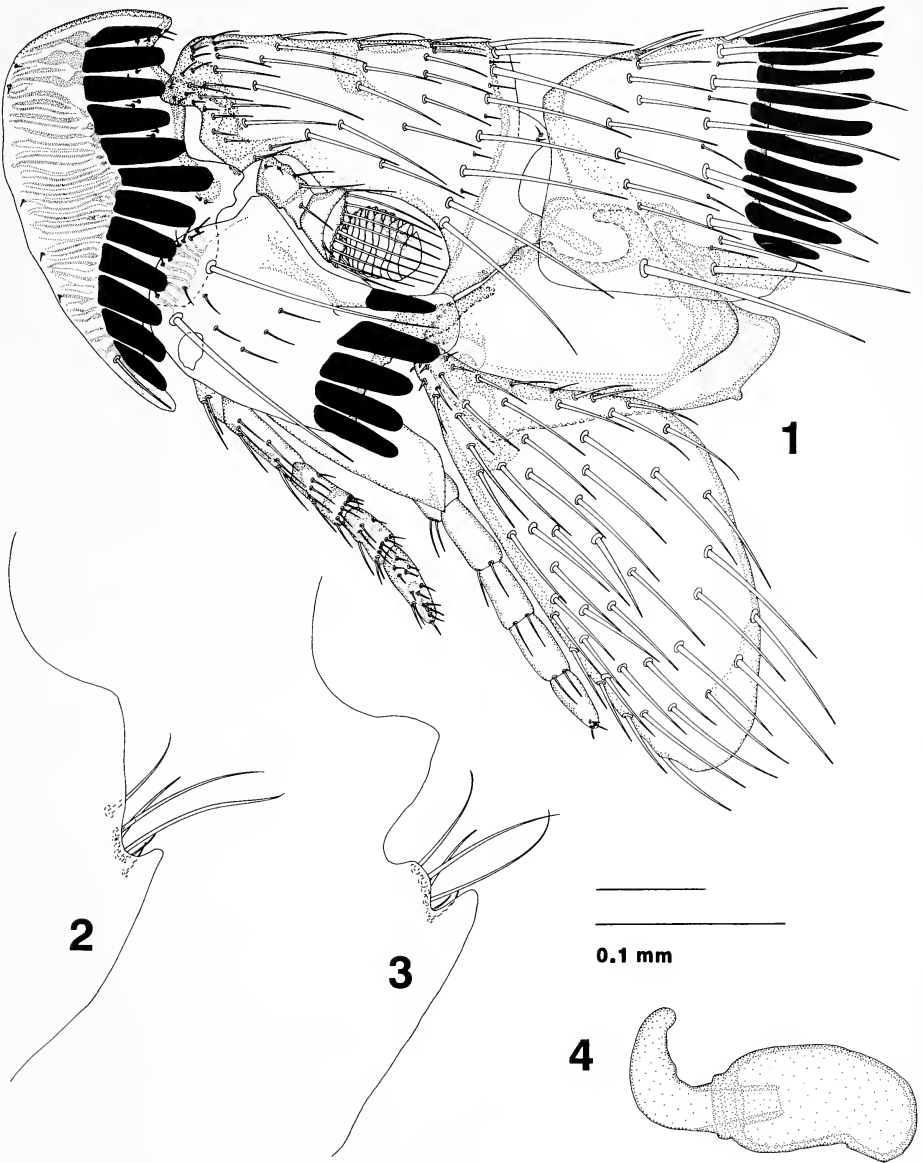
Figs. 1–4.   1. Head and prothorax of holotype female. 2. Posterior margin of tergum VIII of holotype female. 3. Posterior margin of tergite VIII of female *P. lewisi.* 4. Spermatheca of female paratype.

3; II 4/3-4; III 1-2/1-3; IV 0-1/0-1. Sternites II to VI each with several long bristles in a row per side. Sternite VII and tergite VIII with scattered bristles of different lengths. Two long antepygidial bristles per side arising from a slight pedestal. MODIFIED ABDOMINAL SEGMENTS OF FEMALE (Figs. 2, 4). Several long bristles arising below the single prominent lobe along the posterior margin of tergite VIII. Dorsal anal lobe with several long, well-separated bristles per side, lowest long bristle arising from blunt ventro-lateral extension. Spermatheca with deep penetration of hilla into elongate bulga. Hilla similar in length to bulga, with anterior end of hilla extremely narrowed. Anal stylet abruptly tapered, roughly 2.5× as long as its basal width.

Etymology. The specific epithet is the name of a female spirit in the sky, who supposedly could create rain. She was a mythological figure of the Choca Indians, who originally occupied the Pampas region of South America.

Holotype. Female from Mendoza, Argentina, from *Graomys griseoflavus,* 23.VIII.1958, *leg.* D. F. Guménez (BM); 1 female paratype, same data, but 22.VIII.1959 (BM); 1 female paratype from Pilcañu, Rio Negro, Argentina, from *Phyllotis xanthopygus,* IV.1920, *leg.* H. E. Box (BM). All types returned to the British Museum (Natural History), London, England.

Remarks. The type material was designated initially as *P. chiris,* with the specimen from Pilcañu identified as the female paralectotype. We have not selected this specimen as the holotype of *P. kasogonaga* because its abdomen is missing as recorded in Hopkins and Rothschild (1956). Unfortunately, the character involving the arrangement of bristles along the posterior margin of tergite VIII, which separates females of *P. kasogonaga* from those of *P. lewisi,* was also omitted from the original description and illustration by Jordan (1931a). However, the specimen from Pilcañu is assigned to the new species because of the anal stylet, which is abruptly tapered in the original illustration by Jordan, rather than gradually tapered as is characteristic of females assigned to *P. lewisi.*

Of the 24 taxa currently assigned to *Plocopsylla,* five species, including *P. kasogonaga,* have been collected in Argentina. *Plocopsylla kasogonaga* is the only species taken on *Phyllotis xanthopygus,* although four other species of *Phyllotis* are known hosts for members of this genus. This new species and *P. chiris* are the only taxa collected from *Graomys griseoflavus.* This limited host list coincides with the incomplete host data for *Plocopsylla* species in general, which indicates that rodents are the true hosts in this genus, whereas insectivores and marsupials are only occasional hosts (Schramm, 1987).

Besides the type material just listed, there are two additional females listed in the literature that previously have been designated as *P. chiris.* Upon examination, the specimen listed by Mahnert (1982) is actually *P. lewisi* and thus exhibits the same dimorphism with the male lectotype of *P. chiris* as females of *P. kasogonaga.* His specimen is *P. lewisi* because of the bristle arrangement along the posterior margin of tergum VIII and the shape of the anal stylet. Mahnert noted that the anal stylet of his female was less tapered than that illustrated by Jordan (1931a), who had assigned his specimen to *P. chiris.* Here, Jordan's specimen is reassigned to *P. kasogonaga.*

Jordan and Rothschild (1914) identified one female as *Craneopsylla wolffsohni,* although it was later reassigned to *P. chiris* by Hopkins and Rothschild (1956) and

Johnson (1957). This specimen was not examined, but A. K. Thomas (Department of Entomology, British Museum (Natural History)), personal communication, noted that it probably is in the collection of the Zoology Museum in Berlin. If it is *P. chiris,* it will resemble the male lectotype in its prectenidial helmet width, its helmet spines, and in the bristle arrangement. However, there is a strong possibility that it is not this species, in as much as Hopkins and Rothschild (1956) and Johnson (1957) probably used the specimen incorrectly designated as the paralectotype of *P. chiris* for comparative purposes. If there is dimorphism, then the specimen probably is *P. kasogonaga* or *P. lewisi,* both of which have had females misidentified as *P. chiris.* This would result in *P. chiris* becoming one of four species in this genus that are represented by single specimens.

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BEHAVIOR OF SADDLED PROMINENT
HETEROCAMPA GUTTIVITTA (WALKER)
(LEPIDOPTERA: NOTODONTIDAE) LARVAE
IN THE NORTHERN HARDWOOD FOREST

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Abstract. —Feeding and movement of saddled prominent, *Heterocampa guttivitta* Walker (Lepidoptera: Notodontidae) caterpillars were investigated in a northern hardwood forest in upstate New York. The insect is a midseason defoliator. Growth and feeding occur during the warmest and most stable period of year with respect to weather. Weather did not detectably affect feeding or movement behavior. However, total foliage consumption and consumption rate were related to temperature (as determined in the laboratory). The rate of movement between feeding sites increased with older instars. Both feeding and movement exhibited a diel cycle: feeding was greatest during the night, and movement was greatest during the day. Observations are discussed in terms of three currently popular hypotheses explaining caterpillar behavior: that their movement and feeding patterns are a response to weather conditions, variable and unpredictable food quality, or vertebrate predation.

The saddled prominent, *Heterocampa guttivitta* (Walker), (Lepidoptera: Notodontidae) is a periodic defoliator of northern hardwood forests where American beech, *Fagus grandifolia* Ehrh., sugar maple, *Acer saccharum* Marsh., and yellow birch, *Betula alleghaniensis* Britton are principle constituents. During outbreaks, these three species are consistently the most severely defoliated. Species of *Quercus, Populus, Prunus, Hamamelis,* as well as other *Betula* are defoliated to a lesser degree, suggesting that saddled prominent is capable of broad polyphagy. Defoliation reports of some plant species conflict (e.g., *Acer rubrum* L., *Populus deltoides* Bartr. ex Marsh.); however, *Fraxinus* sp., *Tilia* sp. and *Acer pennsylvanicum* L. are clearly unsuitable hosts (Patch, 1908; Martinat, 1984). Outbreaks have occurred in northeastern United States and southeastern Canada every eight to twelve years since 1907. The last major outbreak occurred in eastern Maine where 405,000 hectares were defoliated in 1977 (Martinat and Allen, 1988).

The saddled prominent is indigenous and occurs throughout eastern United States and southeastern Canada. Its seasonal history is well known only in upstate New York and New England (Allen and Grimble, 1970; Martinat, 1984). Here it is univoltine, overwinters as a pupa, and emerges from late May to late June. Eggs are laid singly on the foliage of host tree species selected by the free-flying female. Eggs eclose

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in 9–10 days. First instars skeletonize the lower epidermis of leaves. Later instars feed from leaf margins inward, leaving irregularly shaped uneaten portions. Caterpillars cease feeding 24–48 hours prior to moulting, and remain quiescent on the undersurface of foliage on a silk mat. There are five larval instars, and peak defoliation occurs from mid-July through early August. The period of egg development, eclosion, and caterpillar feeding is therefore approximately early June through early August. Mature caterpillars drop from the foliage or descend tree boles, burrow into the litter below the host tree, and form a loose pupal cell of silk and litter particles. Pupation occurs following a two to three day prepupal period. By mid-August, most caterpillars have pupated.

In an attempt to more clearly understand saddled prominent outbreak dynamics, Martinat and Allen investigated the spatial and temporal aspects of outbreaks (1988), the relationship between outbreaks and drought (1987a), and caterpillar development and survivorship in the laboratory (1987b). Although caterpillar biology and fitness in the laboratory are clearly affected by temperature and humidity, we wished to determine actual conditions experienced by larvae in the forest, and determine if their behavior is affected by changing weather conditions. We therefore studied unconfined caterpillars in their natural habitat, a northern hardwood stand. We report here the results of these observations.

MATERIALS AND METHODS

Studies were conducted from May through August in 1978, 1979, and 1980 at the New York State Ranger School, Wanakena (St. Lawrence County), in an approximately 80-year old stand of pole-sized (12.5–30 cm diameter at breast height) sugar maple and beech. A Foxboro hygrothermograph and Taylor barograph were maintained at the study site. Charts were changed and the hygrothermograph calibrated with sling psychrometer and max/min thermometer weekly from May through September.

Feeding activity and movement. Several hundred first and second instars and eggs were gathered from sugar maple at the beginning of the feeding season and placed on the foliage of several closely spaced sugar maple trees (approximately two per 1-meter branch section, to avoid crowding). Scaffolding with platforms at two and four meters above the ground was placed around the foliage to facilitate close observation. The activity of individual caterpillars was monitored over three to four day periods throughout the season by tagging leaves on which caterpillars were found. They were observed day and night at four to six hour intervals. An observation consisted of recording instar and activity of each caterpillar, approximate portion of leaf eaten since last observed (sketched over outlines on the data sheets), and leaf exposure to sun (in direct sun or shaded). At the time of observation, temperature, barometric pressure, relative humidity (converted to saturation deficit prior to analysis), percent cloudiness, and precipitation (none, light, heavy) were recorded. Individuals which disappeared for unknown reasons between observations were deleted from the data set prior to analysis.

Four to six observations were made within each 24-hour period. Observations continued throughout the summer until larvae completed feeding and vacated the foliage. For analysis, observations were summarized as categorical data per individual (feeding vs. not feeding, moved vs. not moved since last observation, moved within

the same leaf cluster vs. moved to a different cluster, etc.). Data were then compiled into frequency tables and χ^2 tests applied.

Moulting requires one to two days during which the caterpillar remains quiescent and attached to a silken mat on the undersurface of a leaf. A caterpillar found in this condition was assumed to be incapable of feeding or movement, and was therefore subtracted from the total number in the observation.

Foliage consumption. Records of foliage consumption were kept for larvae reared in the laboratory in 8 oz. cups on fresh sugar maple foliage. Approximately 100 individuals were randomly assigned to one of three environmental chambers, the temperature cycles of which were set to simulate the difference in temperature between day (06:00–18:00 hr) and night (18:00–06:00 hr): cycle A, 12.8°C night, 23.9°C day; cycle B, 15.6°C night, 26.7°C day; and cycle C, 18.3°C night, 29.4°C day. Automatic cams on the timing mechanisms of the environmental chambers were cut so that the 5.6°C change occurred gradually over four hours. Fresh sugar maple leaves were photocopied before and after each period of larval feeding, and the amount of foliage consumed was determined to the nearest 0.01^2 inch using a dot grid to measure the amount of foliage removed.

RESULTS

Caterpillar feeding and foliage consumption. Larval development rate is affected by both temperature and humidity (Martinat and Allen, 1987b). Foliage consumption rate is also affected by temperature (Fig. 1). The relationship is most evident during the last two stadia, where about 85% of all consumption occurs.

In the two years of this study, we found few weather conditions in which feeding was not observed. The number of larvae observed feeding was not detectably affected by changing temperature, humidity, barometric pressure, or cloudiness. Larvae were observed feeding in light and moderate rain. Only during intense thunderstorms, which typically lasted no more than 20 minutes, did all feeding apparently stop.

Feeding in all instars exhibited a diel rhythm: greater numbers of larvae were observed feeding at night (19:00–06:00 hours) than during the day (07:00–18:00 hours) (Fig. 2). It is therefore interesting to note that, although consumption rate is temperature dependent, feeding as an activity is apparently not, at least within the range of temperatures observed in the forest during this study. Indeed, feeding activity was greatest during the night when temperatures are typically lowest.

Caterpillar movement. First instars rarely left the leaf on which they eclosed. Later instars moved frequently whether or not the leaf on which they fed was completely consumed. Second and third instars rarely consumed an entire leaf prior to moving, but fourth and fifth instars were sometimes forced to move in response to depletion of local foliage (Fig. 3). Therefore, the frequency of movement increased with caterpillar age. During the day, 65% (N = 134) of fifth instars, 45% (N = 84) of fourth instars, and 35% (N = 73) of second and third instars had moved after six hours, on the average. Movement activity was greater during the day than during the night (Fig. 2). Approximately 80% of all movement by all instars was to a new leaf cluster or branch, indicating that caterpillars frequently bypass local food sources. However, this was also related to instar. Older caterpillars more frequently moved to a distant leaf cluster rather than from one leaf to another in the same cluster (Fig. 4). Fourth
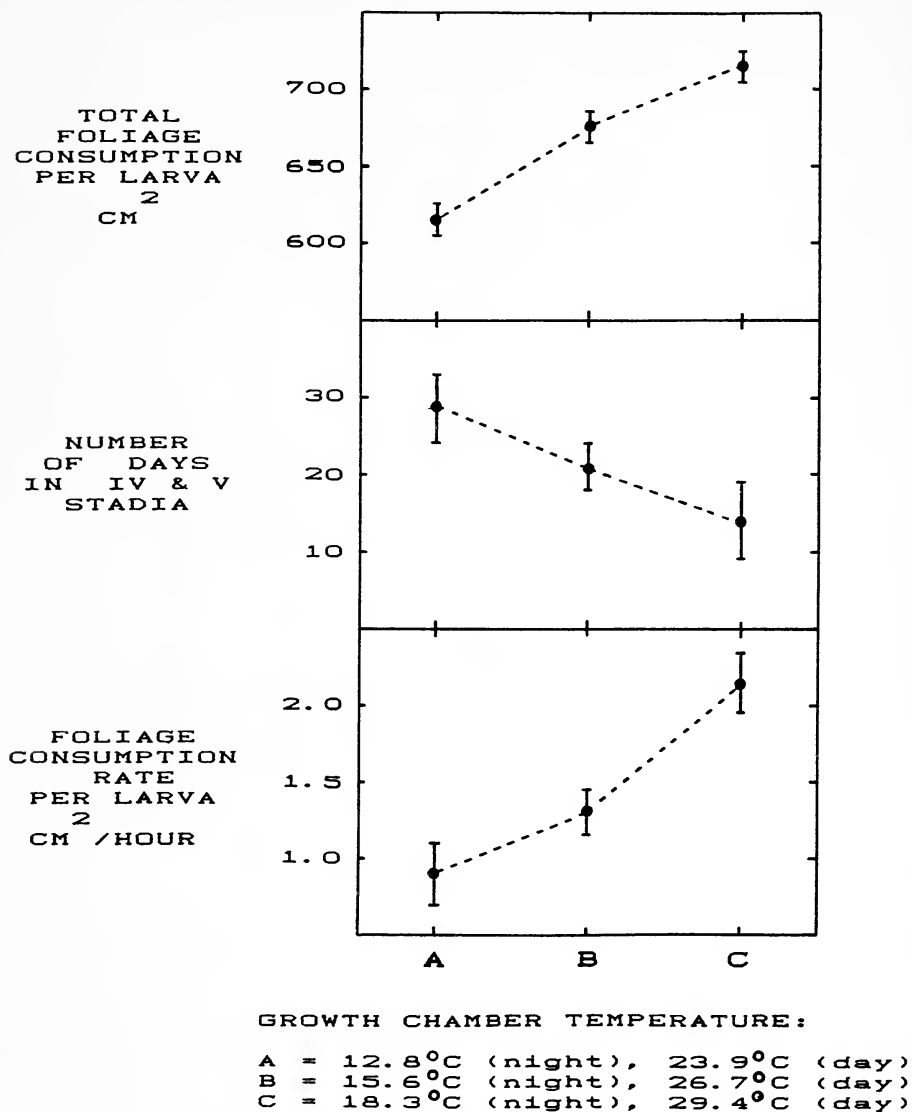
Fig. 1. Foliage consumption of fourth and fifth instars reared under three different temperature cycles. A statistical test (Student-Newman-Keuls procedure, Sokal and Rohlf, 1981) showed that differences in foliage consumption between all three temperature cycles (top graph) were significant ($P < 0.05$).
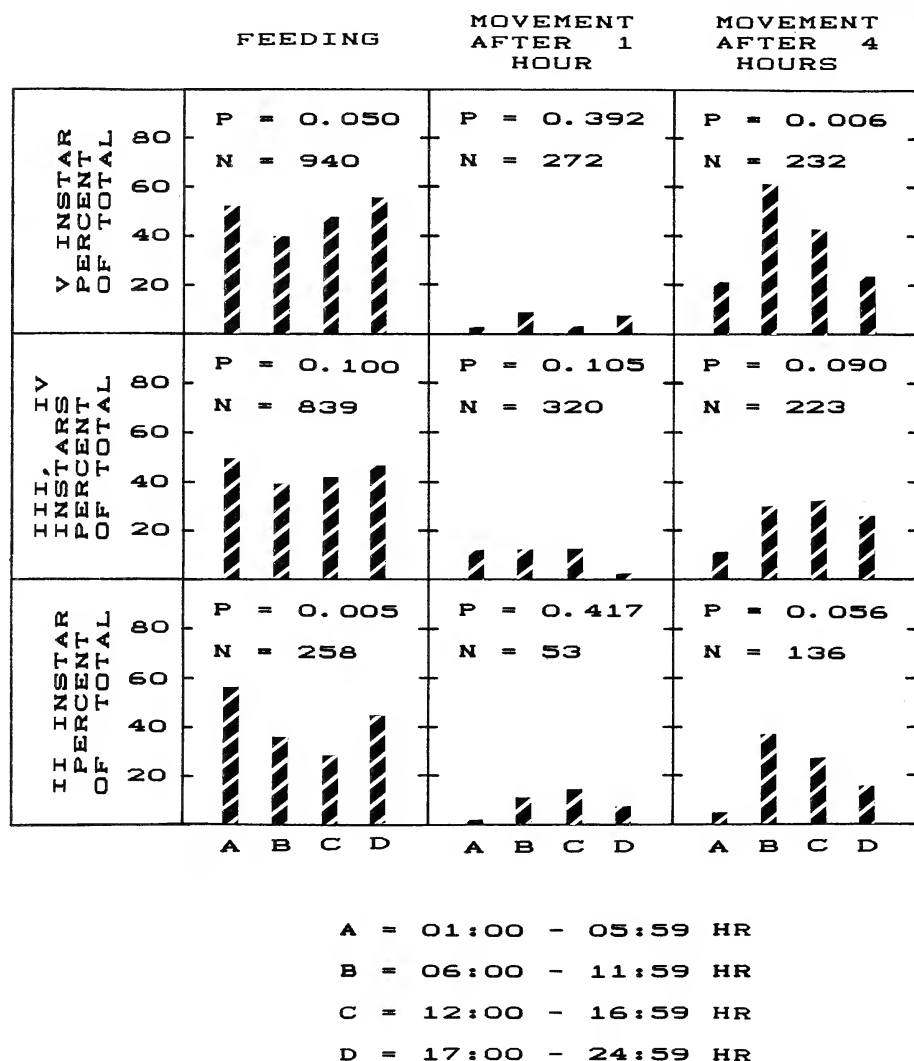
Fig. 2.   Caterpillar diel feeding and movement activity, by instar. Probabilities are those of the χ^2 test statistics obtained in tests of independence (Sokal and Rohlf, 1981).

and fifth instars generally moved longer distances to reach new feeding sites than did earlier instars.

DISCUSSION

In the northern hardwood forest, saddled prominent caterpillar development and feeding occur during the warmest and most stable period of year with respect to weather. During this period, nocturnal temperature minima may occasionally drop
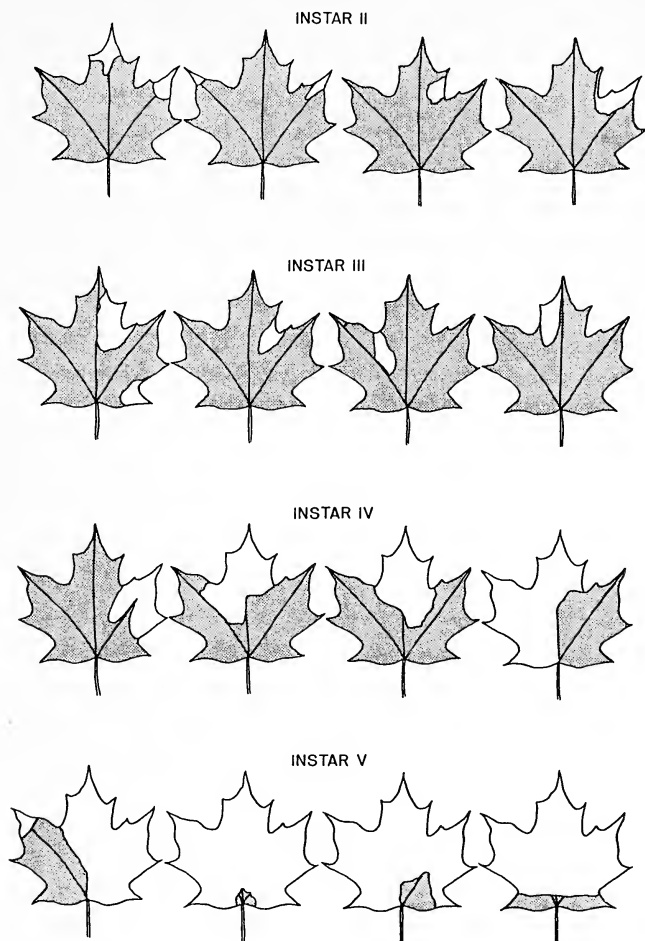
Fig. 3. Sugar maple leaf portions left by saddled prominent caterpillars after they abandoned the leaf in search of another. Leaves of approximately the same size were chosen for illustration.

to 10°C or lower (the temperature at which feeding and movement ceases, Martinat and Allen, 1987b), but caterpillars are exposed to this extreme for no more than a few hours on a given night, at the most. High temperatures or direct solar radiation can also affect caterpillar behavior (Sherman and Watt, 1973; Casey, 1977), but this is also unlikely in our study. Individuals were situated far below the canopy, and thus well shaded. In addition, the average maximum daytime temperature during the hottest two weeks of the summer (16–31 July) was 25.7°C; well below the temperature causing high physiological stress and reduction in development rate or death (Tm, Martinat and Allen, 1987b). Therefore, interruption of feeding due to severe weather conditions is probably rare for saddled prominent larvae.

Early season defoliators are likely to be subject to inclement weather. For example,
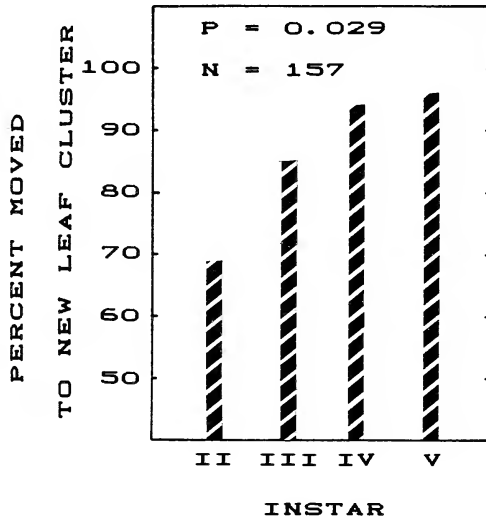
Fig. 4. Percent caterpillars that moved to a new leaf cluster versus the alternative: moved to a new leaf in the same cluster, by instar. Observations were four hours apart. Probability is that of the χ^2 test statistic obtained in a test of independence (Sokal and Rohlf, 1981).

an unusually warm early spring followed by a late spring frost can devastate a forest tent caterpillar (*Malacosoma disstria* Hbn.) population (Blais et al., 1955). In addition, a greater contrast between day and night conditions and a greater frequency of frontal weather increases the unpredictability of daily ambient conditions and reduces the time available for feeding (Wellington, 1954). Similar problems are probably faced by late season defoliators (Morris, 1964, 1967; Morris and Bennett, 1967). A midseason defoliator, however, is less likely to be exposed to inclement conditions. We found this to be the case in our study. We conclude that weather is not the principle cause of caterpillar feeding and movement patterns.

Nevertheless, late instar saddled prominent caterpillars are active wanderers, even in low density populations such as in our study. During the day, they usually remain on a leaf less than eight hours whether or not the leaf is consumed. They often travel several meters to a new cluster and bypass many potential feeding sites. Two alternative hypotheses explaining caterpillar behavior are current in the literature; first, that movement and feeding are a search for optimal but unpredictable food quality (Schultz, 1983); or second, that they are part of a vertebrate predator avoidance strategy (Heinrich, 1979, 1983). Neither of these alternatives alone is a satisfactory explanation of our observations.

Schultz observed that saddled prominent caterpillars accepted only 31% of encountered leaves for sustained feeding, and called them "choosy feeders." Our observations generally concur with Schultz. However, if his interpretation is correct, then not all instars are equally choosy. First instars do not move from the leaf on which they eclose. They do not disperse in the manner of first instar gypsy moths, for example. Initial food plant selection is accomplished by the female when she oviposits. Therefore, first instars must accept the foliage on which they eclose what-

ever its nutritional value, or starve. It may be too energetically costly or hazardous for a first instar to wander in search of food. The high mortality among first instars (Martinat and Allen, 1987b) may then be due to forced acceptance of nutritionally poor foliage. Induction of detoxification systems may occur less readily in early instars (Gould and Hodgson, 1980), and they may be less tolerant of poor food quality (Chan et al., 1978). If first instars survive on less than optimal foliage, the cost may appear as reduced adult fitness.

Heinrich (1979) interpreted a number of saddled prominent behavioral traits as defensive strategies against visually cued vertebrate predators: preference for night feeding, "trimming" leaves rather than leaving leaf shreds, clipping off uneaten portions of leaf by chewing through the petioles (thus removing leaf damage which predaceous birds might use as a cue), and moving away from feeding sites and hiding after bouts of feeding. Except for preference for night feeding, we did not observe these behaviors in our study. In high density populations the forest floor is littered with leaf fragments, but we did not observe "trimming" or "clipping," nor any consistent pattern with regard to which part of a leaf was eaten or what was done with the remainder. Movement was highest during the day and was not away from, but between feeding sites. Caterpillars remained exposed and quite visible throughout the day on twigs and branches as well as foliage.

Although we took no data on predation rates, predation by invertebrates such as foliage inhabitating spiders and *Podisus* sp. (Hemiptera: Pentatomidae) was frequently observed. This casual observation suggests to us that caterpillar movement might just as easily be interpreted as a defensive strategy against invertebrate as against vertebrate predators.

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BOOK REVIEWS

Butterflies

The Monarch Butterfly: International Traveler.—Fred A. Urquhart. 1987. Nelson-Hall, Chicago, 232 pp.

Fred Urquhart began studying *Danaus plexippus* in 1927. Few biologists have had so long a love affair with a single species. Like so many lovers, however, Urquhart became so possessive toward the object of his affections that he claimed exclusive rights to it. In science as in life, therein lie the seeds of trouble. Uninitiated readers will come away from this book thinking that everything we truly know about the Monarch is due to Fred and Norah Urquhart and their associates. Any contribution from unnamed outsiders is invariably a misinterpretation or an error. By failing to place the Monarch in a comparative context, Urquhart creates the impression that it is more unusual or distinctive than it is; even in a popular book like this—albeit with scientific pretensions!—his failure to mention Ackery and Vane-Wright's *Milkweed Butterflies* is nothing short of appalling. It is also typical of what is wrong with this book.

There is no doubt that it was Urquhart's career-long tenacity that led to the discovery of the Monarch's Mexican wintering grounds. That is his great achievement, and he should be proud of it. He has been a meticulous observer and an effective popularizer of his brand of natural history. His outlook has been shaped by a strong dose of Scottish Realism—a profound distrust of "experts" and authority generally, a preference for common sense over theory, and a drive to generate tangible results. These are admirable qualities unless mixed up with obstinacy and obdurateness, as they are here. In "part 9" of this book, entitled "Monarch-Viceroy Mimicry and Bird Predation—Fact or Fiction?" he quotes a set of antique (50–75 years) anti-mimicry-theory authorities, questions the appropriateness of any captive-bird experimentation at all, comes very close to calling certain well-known photographs fraudulent, and acts as if chemical ecology generally were an exercise in fatuous wish-fulfillment. In Scots-Realist style, he invites the reader to see for himself if birds actually attack Monarchs, and draw his own conclusions. Many readers will probably take up the challenge and in consequence conclude that Urquhart is correct in his defiance of an orthodoxy whose spokesmen he does not deign to name. There are in fact both methodological and conceptual problems with that orthodoxy, but the entire chemical-behavioral-ecological corpus is much too large to be blown away by Urquhart's rhetorical posturing, except among those predisposed to his "populist" notion of science. I suppose we should be grateful that he at least accepts biological evolution as credible.

Another distinctive Urquhartism is the coinage of unnecessary jargon, much in the manner of the ecologist Frederick Clements, who called a spade a geotome. In this book we find such florid Fredisms as "exuvial holdfast tubercles," "semi-exar-

ate," "posculum and patella," "transient hibernal roosting loci," etc. On p. 51 he says "In scientific publications the gold spots (of the pupae) are referred to as 'prismatic pigmented maculae' "—not bothering to add that he is the only one doing the referring. On p. 122 he defends his coinage "alar tagging" by saying the word "alar" is "well-known among scientists working in many different languages." (So is "wing.") In the caption to plate 4, he uses the familiar word "prepupa" in a new and totally unwarranted sense to refer to the untanned pupa *after* molting. And so on.

For a hard-headed anti-theoretician, Urquhart indulges in such vapors as this: "Eventually through some evolutionary process, the east–west movement was incorporated into the monarch's genetic code to produce a cyclical migration related to some as yet unknown response to seasonal changes on the planet" (p. 120). No French Structuralist could say less in so many words. His quantitative sophistication is demonstrated by the out-of-context and utterly meaningless egg-distribution data presented on p. 89 (under the misspelled heading "ov*a*position"). This is a statistically difficult subject, which Urquhart handles by ignoring statistics altogether.

The book contains numerous errors, some trivial, some significant, all of them annoying. San Luis Potosí, with at least 300,000 people, is not a "small village" in Mexico (p. 154). The roosting tree of the Mexican winter sites is the Oyamel, *Abies religiosa*—a fir and not a "spruce" as Urquhart always calls it (p. 156 ff.). Braconids are not "bees" by any reasonable definition (plate 20, caption). And so on. After a lifetime studying the Monarch, why does Urquhart claim in the caption of his range map (p. 129), and reiterate in the text (p. 137), that the breeding range of the western Monarch population is the "valleys of the Rocky Mountains," by implication exclusively? Anyone finding Monarch larvae in his back yard in the Great Basin, California or the Pacific Northwest would be justified, based on this book, in thinking he had a major range extension in hand. Over 25 years ago I watched Monarchs migrating north through Albuquerque, New Mexico in May; yet Urquhart doesn't show them in that state *at all*. Indeed, one gets the impression he credits no data not gathered by himself, and consults as few published sources as he can get away with.

Quite a few of the citations in the short bibliography are incorrectly given. There is no such journal as the *Journal of the Lepidoptera Society,* used repeatedly. The heading "scientific papers" embraces both legitimate papers in refereed journals and popular articles in *National Geographic.*

In Appendix B Urquhart provides a list of butterfly species tagged by his observer network, and concludes that—except for three conspicuous, well-known migrants on the Gulf Coast—the Monarch is our only true long-distance migrant. Most of the species he lists have never been suspected of long-distance migration by anyone not under the influence of mind-altering substances. Of those that have, most probably *are* seasonal migrants. Certainly the Painted Lady (*Vanessa cardui*) is. Since Urquhart does not describe the design of his tagging schemes, let along give numbers tagged, seasons, or circumstances, there is no way to evaluate the effectiveness of his methods or their probability of generating returns. Again, the unsophisticated will be misled by glib rhetoric.

This is an infuriating book. One wants to be nice to the grand old man who tracked the Monarch to its lair, but how can one ignore his pigheadedness and egocentricity? Except for the scrambled order of states in Appendix C, this is a beautifully-produced book, nearly free of typographical errors; its production values are better than its

content. It has numerous color plates, expensive to produce and utterly unnecessary; most lovingly reproduce all the flaws in series of badly-mounted Monarchs to no obvious purpose. How typical! What a pity!—*Arthur M. Shapiro, Department of Zoology, University of California, Davis, California 95616.*

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Ackery, P. R. and R. I. Vane-Wright. 1984. Milkweed Butterflies. Cornell University Press, Ithaca, New York, 426 pp.

The Butterflies of Indiana.—Ernest M. Shull. 1987. Indiana University Press, viii + 262 pp., 50 pls. $25.00 cloth.

In the past several years there have been a number of publications on the butterflies of various states, and more are to be published. Some leave quite a bit to be desired, while others stand out as examples of how these should be done. Shull's work on the Indiana fauna definitely falls in the latter category, and is perhaps the best state compendium that I have seen.

The introduction includes sections on the biogeographical areas of Indiana (with an accompanying map), biology in the broad sense (including color patterns, mimicry, migration, and the sap-feeding species), collecting, classification and identification (plus a list of the major museums and collections in North America), plus conservation and the endangered species act. The bulk of the book is taken up with the species accounts, giving diagnoses, distribution (having a state map showing the counties in the margin beside each species) and habitat, plus life history notes. Food plants are given for each species where known; these are not restricted to just Indiana. Shull has spent some three decades collecting in Indiana, and so he is well qualified to comment on the occurrence, nectaring, and flight habits; he lists every pair of mating butterflies he has observed, complete with locality, time and temperature data. These observations add welcome information for the 149 species known to fly in Indiana.

Interspersed in the text are the colored photographic plates that show every species of skipper and true butterfly; 535 specimens are illustrated, with both sexes and the under surface of the wings usually being given. In general, the color work is excellent; in a few cases the red appears to be a bit too strong, and there are a few small dark spots on a number of the plates.

At the end is a check list of the species, a "hypothetical list" of butterflies that may show up in the state (one more possible addition might be *Phyciodes pascoensis/ morpheus*), a short glossary, the literature cited, and separate indices to food plants and the butterflies.

A couple of minor errors might be pointed out, such as "genuses" in the caption for figure 4, and Shull's statement that the Cabbage White is the only Indiana butterfly that has been found in all 92 counties, although its presence is not indicated on the accompanying map for De Kalb County.

The entire book is on heavy coated paper. With all the information it contains, with all the color photographs, and with its inexpensive price, this book is definitely a bargain. Shull and the Indiana Academy of Sciences are to be congratulated on a job well done.—*Frederick H. Rindge, Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024.*

Taxonomy, Phylogeny, and Biogeography of *Asterocampa* Röber 1916 (Lepidoptera, Nymphalidae, Apaturinae).—Tim Friedlander. *Journal of Research on the Lepidoptera,* 31 Dec. 1987 25(4):215–338, 13 figures, 11 tables, 22 plates. Available % Santa Barbara Museum of Natural History, 2559 Puesta Del Sol Road, Santa Barbara, California 93105.

This is an important work for lepidopterists, systematists and biogeographers because of the variety of data sources and methods used to determine results. Friedlander's study comprises an entire issue of the *Journal of Research on the Lepidoptera* in monographic format.

Friedlander's work, refined from his 1985 doctoral dissertation at Texas A&M University, is essentially a completion of research originally initiated by the late Dr. Walfried J. Reinthal of Tennessee. Reinthal studied *Asterocampa* ("Hackberry Butterflies") for many years, hand-pairing, rearing and cross-pairing many of the Nearctic taxa. As Friedlander notes, results of Reinthal's work (communicated mostly through correspondence) were widely cited by lepidopterists in systematic and faunal studies. The meticulously catalogued Reinthal collection (willed to the Carnegie Museum of Natural History) served as a major reference in Friedlander's research. The time elapsed in the Reinthal and Friedlander studies can be illustrated by my mentioning that twenty-four years ago I sent live ova to Reinthal for rearing and cross-pairing of the western Great Plains *Asterocampa*!

Rarely in works concerning Lepidoptera (or entomology in general) is cladistic methodology applied to data including (i) morphology of adults *and* immature stages, (ii) life histories and foodplant relations, (iii) behavior, (iv) cross-pairing/rearing experiments and (v) biogeographic data. Revisionary works normally utilize some of these data; then workers debate what alternative results might have been possible with more data. Consequently, in recent years, no other issue has divided lepidopterists more than morphological versus biological species definitions and how to apply the obligatory categories of the Code of the International Commission on Zoological Nomenclature. Thus, as an example of how such various data sources affect a cladistically-based revisionary study, the *Asterocampa* monograph is a seminal work. Friedlander is aware of this, amply addressing how various data bases, and methodological views, might affect the study. There is no particular prejudice in how he proceeds.

The monograph treats a relatively small monophyletic group. Four species are recognized, with a distribution including the Nearctic plus Mexico and the Antilles. For butterflies, the group is particularly non-vagile. *Asterocampa* are well documented "perching" (versus "patrolling") species, with adults notably restricted to foodplant

micro-habitats. With such a small group, available data per taxon for the Nearctic species is about even. Unfortunately, the exception to this balance—lack of comparable data for evaluating reproductive isolation in the Antillean and Mexican *Asterocampa*—leaves unresolved a major question concerning the taxonomy and evolution of this group.

Taxonomic sections are compact, with keys provided for adults, larvae, pupae and eggs. Synonymies and general literature citations are rather abbreviated (the author frequently referring the reader to materials in the 1985 dissertation). Discussion of materials and methods is detailed, with sections summarizing morphological, biological and behavioral data along with cross-pairing/rearing experiments. Synthesis of results appears in two sections, "Phylogeny" and "Biogeography." In the phylogenetic analysis, the PAUP computer package and Wagner Tree method are applied to a 20-Character by Outgroup + 10-Taxa data matrix and their results compared. Characters include egg, larvae, pupae and adult morphology (including wings and genitalia), host plant data, behavior and geographic distributions. The outgroup consists of other taxa of the Apaturinae, *Asterocampa* being considered the sister group of Old World *Chitoria, Dilipa, Euapatura,* and possibly *Thaleropis.*

A Wagner Tree from these data indicates four terminal groups and is congruent with the four terminal branches of a diagram produced by PAUP for the outgroup plus ten subspecific taxa. Friedlander determines the presence of four "species" based on the congruence of the four taxon statements and what is experimentally known concerning reproductive isolation. He acknowledges that, cladistically, reproductive compatability is a symplesiomorphy; thus, he considers experimentally-documented reproductive isolation a possible synapomorphy. This approach is new in lepidopterology and may set a precedent for studies which contain experimental data on reproductive isolation. As Friedlander notes, previous treatments of *Asterocampa* based on wing pattern and morphology had included upwards to twelve species.

Friedlander recognizes two major clades within *Asterocampa*: (i) the "Celtis Group" (polytypic Nearctic *A. celtis* and relatively homogeneous Mexican/SW United States *A. leilia*), and (ii) the "Clyton Group" (relatively homogenous Nearctic *A. clyton* and polytypic Mexican/Antillean *A. idyja*). The "Celtis Group" is assessed as having the most advanced characters with the "Clyton Group" considered relatively plesiotypic. In comment, Friedlander notes he is including within *A. idyja* phenotypically dissimilar Mexican and Antillean populations, the former being notably mimetic but not the latter. He remarks that character differentiation was perhaps poorest for the *A. idyja* complex and that no cross-pairing/rearing experiments were possible with these taxa.

The phylogenetic results lead to great interest in the author's assessment of biogeography. Friedlander's choice of *Chitoria* dispersal across a Bering Land Bridge as the origin of Nearctic *Asterocampa* is slightly disappointing. From reading his literature review, one cannot help think he really meant vicariance of ancestral *Chitoria/ Asterocampa* populations already in place (especially since another endemic New World apaturine assemblage, *Doxocopa,* is acknowledged as having evolved in such a fashion).

Concerning speciation within *Asterocampa,* Friedlander argues convincingly that vicariance of the geographically sympatric "Celtis" and "Clyton" groups resulted not

from macro-geographic separation but by divergence of oviposition and host plant strategies. Restricted to respective "new-growth" and "old-growth" oviposition and feeding habits, members of the two groups segregate into distinctive micro-habitats. With similar clarity, Friedlander attributes speciation within the "Celtis Group" to the xeric (southwestern U.S./Mexican) adaptation of *A. leilia* coupled with a series of Pleistocene isolation events forming components of polytypic *A. celtis.*

Clarity concerning Antillean/Mexican allopatry is, however, more problematic. Here, Friedlander has an understandable lack of good data and many presuppositions of current lepidopterology working against him. He is stuck with his subspecies clustering of Antillean nominate *A. idyja* and Mexican *A. idyja argus,* but also with the reality of *Asterocampa* being apparently poor dispersers. Here, in an otherwise elaborate study, it is truly unfortunate that character and cross-pairing/rearing data were not available for the Neotropical taxa. Based on the sister group status of these populations from the Wagner and PAUP data, Friedlander can only extrapolate possible reproductive potential from its occurrence in the Nearctic *A. clyton* complex. Thus, his speculation that *A. idyja* and *A. argus* are conspecific will be controversial. Because of these circumstances, Friedlander chooses a compromise vicariance/dispersal explanation for the origin of Antillean *Asterocampa*—since the Antilles are too old for the speculated age of *Asterocampa,* over-water dispersal to the Antilles must have taken place at a time when tectonic actions had moved the Antilles only a minimal distance from the mainland.

Future cladistic data on Caribbean butterflies may alter this common view that the Greater Antilles are too old for tectonic vicariance to have caused speciation in their butterfly faunas. By rigorous character analysis, the most recently discovered fossil Nymphalidae, from the Oligocene, appear to be congeneric with modern taxa (L. D. and J. Y. Miller, 1988 presentation to 39th Annual Meeting of the Lepidopterists' Society). This pushes back even farther lepidopterists' views of how ancient certain contemporaneous lineages may be. With the Friedlander monograph, published cladograms are available for three groups of mainland/Antillean butterflies: *Asterocampa, Anetia* (Danaidae) (P. R. Ackery and R. I. Vane Wright, 1987, Milkweed Butterflies, Their Cladistics and Biology. British Museum (Natural History) / Cornell Univ. Press, vii + 425 p.) and *Nesiostrymon/ Terra* (Lycaenidae) (K. Johnson and D. Matusik, 1988, Ann. Carnegie Mus. 57:221–254). All three groups have terminal assemblages with mainland/Antillean bifurcations, and each contains notably micro-habitat restricted or non-vagile butterflies. A cladogram for the extremely vagile Neotropical "Prepona" butterflies (Nymphalidae) (ms. in prep. by me and Henri Descimon (Universitie de Provence, France) indicates that only members of its relatively primitive stem (*Archaeoprepona*) occur in the Antilles. The latter is somewhat surprising, considering the species richness of the more structurally advanced sister genus *Prepona.* If over-water dispersal was a common phenomenon among butterflies, it would seem as likely that *Prepona* would also have Antillean representatives. Thus, one comes away from Friedlander's *Asterocampa* scenario aware of his predicament, but somewhat unsatisfied.

Obviously the "jury is only beginning to come in" concerning cladistics, vicariance, dispersal and Antillean butterflies. However, cladograms to date do not provide obvious examples of dispersal and contain, at least, strong hints at geographic vicariance. Friedlander's data on New World *Asterocampa* are one piece in this puzzle

and his monograph gives a rich background upon which someone can attack the apparently open issue of Antillean biogeography and Hackberry Butterflies.—*Kurt Johnson, Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024.*

Behavior

Evolutionary Genetics of Invertebrate Behavior.—M. D. Huettel (ed.). 1986. Plenum Press, New York, ix + 335 pp. $59.50.

Mayr (1963) has argued that evolutionary transitions to new niches or adaptive zones are generally initiated by changes in behavior. Given this and the bewildering diversity of invertebrates, both in terms of species numbers and ecological niches occupied, studies of the genetics of their behavior should contribute substantially to our understanding of the biological world. The present volume brings attention to the potential importance of such studies and, I hope, will serve to attract more students into this field. It comprises 30 chapters contributed by well-known figures in the fields of behavioral genetics and evolutionary ecology. The general areas covered include: (1) genetic variation in natural populations for courtship and mating, oviposition behavior, non-reproductive interactions among conspecifics, and life history traits; (2) molecular and biochemical genetics of behavior; and (3) some theoretical considerations of the role of behavior on evolution and speciation. Thus, a lot of important ground is covered.

Unfortunately, this volume has some serious shortcomings. First, it is quite narrowly focused with respect to the organisms and topics covered. All of the empirical chapters except one, which considers egg laying behavior in *Aplysia,* are concerned with insects and spiders, and 10 of these deal with *Drosophila.* A number of important topics, such as dispersal polymorphisms, insect social behavior, kin recognition, and general habitat selection, are not covered.

A second problem is that the book was out of date by the time it was published. This volume is the outcome of a meeting that was held in March of 1983, yet the proceedings were not published until 1986. Only three of the chapters included references to papers that appeared after 1984, and one refers to a paper that actually came out in 1983 as "in press."

Other oddities include chapters that do not deal with or mention behavior, such as that by Scriber et al. on color polymorphism in tiger swallowtails and that by Slatkin and Kirkpatrick on the general use of quantitative genetics for evolutionary studies, and a reference by Carde to "Teal et al. (this volume)," a non-existent chapter.

Finally, the quality of the science in many studies of the evolutionary genetics of behavior, including some in this volume, leaves something to be desired. The most serious problems are lack of true replication of experiments, and making genetic intepretations based on small sample sizes without taking into consideration the power of statistical tests used. For instance, suppose one crosses two interfertile species and then backcrosses the hybrids to one of the parents. If, in the backcross

progeny, 7 resemble the hybrid and 12 resemble the parental species, this is not strong evidence for monogenic control of the trait being considered, even though the numbers obtained do not differ significantly from a 1:1 ratio. Similarly, an observed genetic correlation between two traits of -0.29 ± 0.28, which is not significantly different from zero, does not necessarily mean that the correlation is actually zero and that the two traits can evolve independently.

Despite these complaints, this collection should be perused by evolutionary biologists who are interested in any aspect of behavior. Those who do are likely to find that one of the variety of approaches employed by the contributors, from mosaic analysis to quantitative genetics, may be particularly suitable for studies of their own favorite organisms.—*John Jaenike, Department of Biology, University of Rochester, Rochester, New York 14627.*

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Perspectives in Chemoreception and Behavior.—R. F. Chapman, E. A. Bernays and J. G. Stoffolano, Jr. (eds.). 1987. Springer-Verlag, New York, New York, 206 pp. $59.00.

Vincent Dethier is well known as one of the foremost investigators in the area of insect behavior and chemoreception. This volume is the result of a symposium held in honor of his 70th birthday, at the University of Massachusetts, Amherst, in May 1985. Papers by his colleagues and collaborators address the diverse areas of investigation to which Dr. Dethier has made fundamental contributions during his career.

L. M. Schoonhoven's chapter describes the chemosensory equipment of caterpillars and provides a comprehensive, current review of the search for an understanding of the sensory code, which tranlates the responses of a caterpillar's small number of chemoreceptors into host-specific feeding behaviors. F. E. Hanson describes the structure and neurophysiology of the contact chemosensory hair of muscoid flies (*Phormia* spp. and *Calliphora* spp.). Hanson's chapter emphasizes current theories of the mechanisms of taste stimulation for the four dendrites found in the hair and also includes speculation about a sensory code in these flies. T. Jermy provides a brief, clear review of our knowledge of feeding preference induction, oviposition preference induction, sensory and CNS-based habituation and food aversion learning in phytophagous insects. A short chapter by A. Gelperin contributes to this theme with interesting recent information on associative learning in the blowfly (*Phormia*), and the methods of its investigation.

Other chapters on insect/plant interaction include D. Schneider's description of the fascinating physiological and ecological relationships between certain danaids and arctiids and the pyrrolizidine alkaloids of their host plants. R. F. Chapman and E. A. Bernays present a well developed argument for viewing the evolution of insect aversion to certain plant secondary compounds as driven by a variety of ecological

and physiological factors rather than just the toxicity of these compounds. They point out that the 'deterrent receptors' found in many insects are broadly sensitive to many compounds not normally encountered by these insects and that this leads to rejection of novel diets, whether or not this rejection is ecologically or physiologically adaptive. This chapter is particularly stimulating because it provides an evolutionary context for our knowledge about the insect chemical receptor system.

J. S. Kennedy describes Dethier's experimental search for the existence of 'motivation,' an elusive concept related to the endogenous factors influencing an animal's response to a stimulus. Dethier ultimately rejected the concept as only a metaphore for emergent properties of more complex CNS integration. Kennedy uses the discussion to issue a warning that 'mentalist' or teleological language is still prevalent in the behavioral sciences. He argues that such terms are misleading impediments to understanding behavioral mechanisms. Although this warning is an old one, it bears repeating.

M. Rothschild presents data and qualitative observations of oviposition by *Pieris brassicae* and offers a tenuous, and by her own acknowledgement speculative, adaptationist hypothesis for this complex behavior. Her interpretations are not convincing, but this chapter serves as a reminder, to those currently involved in similar research, of the difficulties in interpreting the complexities and variability of insect behavior.

There are two chapters (C. Pfaffmann and L. M. Beidler), on mechanisms of vertebrate gustation and one (E. Stellar) describing a method of quantifying appetitive motivation in the rat. Although their inclusion is consistent with the general theme of the book, they seem somewhat out of place in a work otherwise devoted to insects. A more general treatment of vertebrate chemosensory research, including conceptual links to insects, would have been appropriate in a volume likely to attract more entomologists than vertebrate physiologists. L. M. Beidler comes closest to such a synthesis by including a comparison of the response attributes of several vertebrate taste receptors and those of the blowfly.

The diversity of topics included in this book reflects the remarkable breadth of Dr. Dethier's influence on behavioral, physiological, and evolutionary biology. The breadth of this small volume, however, makes it somewhat disjointed, and few readers will find all of the book interesting. Another problem, common to symposium volumes, is that some of the material is dated. Although most of the chapters have been revised since their presentation as papers, few references (13, by my count) are more recent than 1985.

A charming aspect of the book is the admiration of the authors for Dr. Dethier's research and for his fascination with insect behavior. This admiration is reflected in the quality of the individual chapters and provides continuity to this tribute to his work.—*S. D. Eigenbrode, New York State Agricultural Experiment Station, Geneva, New York 14456.*

J. New York Entomol. Soc. 96(4):487–489, 1988

The Natural History and Behavior of North American Beewolves.—H. E. Evans and K. M. O'Neill. 1988. Comstock Publishing Associates, Ithaca, New York, vii + 278 pp. Cloth $45.00, paper $23.50 U.S.

The Natural History and Behavior of North American Beewolves, with some exceptions, follows the content pattern of H. E. Evans' similar books on sand wasps (1957, 1966). The treatise on beewolves places more emphasis on male behavior and male mating strategies than these earlier books.

A well-written Introduction gives an excellent overview of the biology not only of beewolves of the genus *Philanthus,* but also provides valuable information about male and female sphecid wasps in general. The historical perspective of this section is particularly enlightening for readers who know little or nothing about insect or wasp behavior. Table 1-1 presents biological information at a single glance for this group of wasps. Chapter 2 reveals the major features of behavior common to most species of *Philanthus,* with emphasis on the European and African *P. triangulum.* The groundwork for subsequent chapters on individual groups and species is cemented together in Chapter 2, and many terms and concepts employed throughout the text are defined therein. Subsections entitled Habitat and Life History, Male Behavior, Female Behavior, Nest Structure, Provisioning, Natural Enemies and Economic Importance are so concisely written that they could serve as models for subsequent studies on these aspects of behavior in other groups of wasps.

Chapters 3, 4, 5 and 6 provide significant, detailed information on male behavior, burrow sharing, nesting behavior and natural enemies for 19 species in the *Philanthus zebratus, gibbosus, pacificus* and *politus* Groups, respectively. Each chapter is well illustrated with photographs and diagrams, and contains much tabular information. Certain aspects of the behavior of some of the species are covered thoroughly, e.g., male behavior in *P. bicinctus, P. basilaris, P. crabroniformis* and *P. pulcher,* and provisions of *P. zebratus* and *P. pulcher.* Chapter 7 utilizes the same approach and subheadings as Chapters 3–6 in treating five additional North American species of *Philanthus.* Evans and O'Neill place these five species in this chapter because they "form a diverse lot structurally" and are unrelated to species in Chapters 3–6. They indicate that these species had been assigned previously to four species-groups and perhaps the authors should have used these assignments here to conform to the ordering of the groups in Chapters 3–6. There appears to be enough behavioral information given to warrant tentative assignments despite the fact that Evans and O'Neill indicate that none of the species has been "thoroughly studied."

Chapter 8 furnishes a brief review of behavior of five Eurasian species of *Philanthus,* but only the widely distributed *P. triangulum,* the so-called beewolf of Europe and Africa, is treated in any detail. One of the strengths of this book is the chapter (9) entitled "An overview of male mating strategies." So few compilations on behavior in sphecid wasps have paid attention or given just due to the intricacies of male behavior and mating strategies; hence this chapter is extremely timely. A wide variety of subtopics treat little investigated yet highly interesting facets of the male's participation and contribution to the total behavioral picture in sphecid wasps. Particularly interesting and significant topics in this chapter include scent-marking, aggressive interactions, intraspecific body size and mating success, individual male tactics, associated costs and intersexual selection. Tables 9-1 and 9-2 bring together much information on male behavior and territoriality in other genera of sphecid wasps.

In Chapter 10 Evans and O'Neill synthesize existing information on the behavior of species of *Philanthus* and speculate on the evolution of behavior patterns within the genus in relation to what is known about the evolution of behavior in other

wasps. A series of tables and diagrams helps to explain variation in some of the individual behavioral components. This chapter concludes with a definition of ancestral and derived behavioral characteristics within the subfamily Philanthinae and a flow chart that depicts aspects of the evolution of male and female behavior in digger wasps.

This is a highly organized, well-written, easily readable book detailing the individual behavioral components of males and females of the sphecid genus *Philanthus*. It approaches the subject from the standpoint of evolution of behavior in digger wasps and is synthetic in scope, tying together a myriad of significant information ranging from scent marking, alternative mating strategies and body-size related to success in mating in males to construction of false burrows, nest aggregation and counter-cleptoparasitic behavior in females. Anyone with an interest in descriptive and evolutionary behavior, behavioral ecology or natural history will want to purchase, read and place this very informative and highly interesting book on their shelf. — *Frank E. Kurczewski, Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, Syracuse, New York 13210.*

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Mostly Flies

A Manual of Forensic Entomology. — Kenneth G. V. Smith. 1986. British Museum (Natural History) and Cornell University Press, 205 pp. $39.95.

Smith has written an engaging and very readable primer on forensic entomology — the first in English. The aim of the author is to simplify complex material and to serve those with only an elementary knowledge of entomology. He succeeds with a style that is direct, engaging and lucid, perhaps best exemplified in the keys to the mainly European insect fauna found on corpses and the excellent diagnostic drawings. The book has chapters on the faunal succession on cadavers, methods and techniques, case histories, keys and illustrations of relevant Diptera species, and illustrations of species of Coleoptera, Hemiptera, Lepidoptera, etc., and even of Cannabis insects. The glossary is a useful adjunct.

One might conclude from a first reading that with an elementary knowledge of entomology and this manual, an individual would be ready to tackle homicide cases. Nothing could be farther from the truth. Indeed, a little knowledge could be a dangerous thing. Forensic entomology is a specialist field. It should not be practiced by persons with only an "elementary knowledge of entomology," especially when lives may be at stake, as in homicide cases. The following will serve to illustrate some of the complexities involved and sophistication required.

Faunal successions on carcasses do not operate like clockwork and the longer out one goes the less precise become the schedules of arrivals and departures. Uncritical reliance on successional data to pinpoint the postmortem interval could result in significant error. Furthermore, one cannot automatically transpose successional data from lizards, guinea pigs, dogs, cats, rabbits, pigs, etc. to human corpses. The difference in biomass alone could alter the picture, to say nothing of the interactions with abiotic factors e.g., temperature, wind, rain and/or ground moisture, and sun/shade. Table 4 is taken from Nuorteva (1977) and is a case in point. The table presents data on the duration of development of some blow flies in fish in the field in Finland. The following factors which could influence the rate of development are not given.

1. Amount of fish. This constrains the number of maggots. A large maggot mass would elevate the temperature and accelerate maggot development. Possible drying out of the fish could prolong larval development.

2. Temperature. Only the mean temperature from a meteorological station at an unspecified distance is given. The real temperature history of the maggots in the field is unknown. Would we be justified in transposing the data in this table to a case involving a human homicide? I think not.

It will be confusing to the novice to find that Table 5 gives egg–adult development time of *Calliphora vomitoria* as 21 to 27 days while Table 6 gives it as 12 to 13 days. Table 6 does not give a rearing temperature while Table 5 does. This is a small but significant omission because developmental rates are temperature driven. Table 5 is taken from Kamal (1958) and the modes for most species do not add up to the totals that are given. Some experienced dipterists have consulted Kamal's original dissertation and note that the reared flies in the photographs are only about one half to three quarters the size of wild flies in the same area. It is possible that the rearing media were allowed to dry out or the amounts were insufficient, thus prolonging the larval stage. Nuorteva (1977), unfortunately, includes the same table. One wonders in how many forensic cases the data in this table have been used.

Smith points out the importance of temperature in controlling oviposition and development of sarcosaprophagous insects and cites Reiter (1984) as follows: "He also found that constant temperatures over 30°C led to stunted forms which failed to pupate and died. . . ." Smith does not mention that this observation refers specifically to *Calliphora vicina*. The reader may conclude erroneously that this is true of blow flies generally, which it is not.

A few paragraphs later is the following statement. "Thus, on bodies found indoors one would normally expect to find *Calliphora,* but not *Lucilia* or *Sarcophaga* (unless all the windows were open and the body in bright sunlight)." I have found *P. sericata* larvae on bodies in these situations: pitch black bathroom; room with a northern exposure with windows closed and shades drawn; trunk of a car; and causing myiasis in patients in a screened hospital room and in a hospital ward without direct sunlight. The drive to oviposit will cause 'heliophilic' species to do strange things.

Two technical trivia. On p. 53, ". . . the third stage larva forms a puparium from its cast skin. . . ." Actually, the puparium is formed before the skin is cast and the skin is not cast until the larva (=prepupa) molts to the pupal stage. On p. 50, third line up from bottom: 231 ft = 6.5 m?

It is about 100 years since Megnin pioneered the field of forensic entomology by

describing eight stages in the decomposition of a human corpse and the insects associated with each stage. Forensic entomology is still a young science and precisely for this reason it must maintain rigorous standards among its researchers and practitioners if it is to gain widespread acceptance. There is no substitute for good data, nor for well-trained entomologists to interpret and apply them. This book does a good job of opening the door but invites the wrong people in. 'Mathematics for the million' is fine, but maggots for the million won't hold up in court.—*Bernard Greenberg, Department of Biological Sciences, University of Illinois at Chicago, Chicago, Illinois 60680.*

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1988

REVIEWERS

INSTRUCTIONS TO AUTHORS

The *Journal of the New York Entomological Society* is devoted to the advancement and dissemination of knowledge of insects and related taxa. The costs of publishing the Journal are paid by subscriptions, membership dues, page charges, and the proceeds from an endowment established with bequests from the late C. P. Alexander and Patricia Vaurie. The Journal will consider for publication manuscripts of any length dealing with original research in entomology. Longer papers will be printed as articles, shorter ones as "scientific notes." Book reviews will be solicited by the Book Review Editor.

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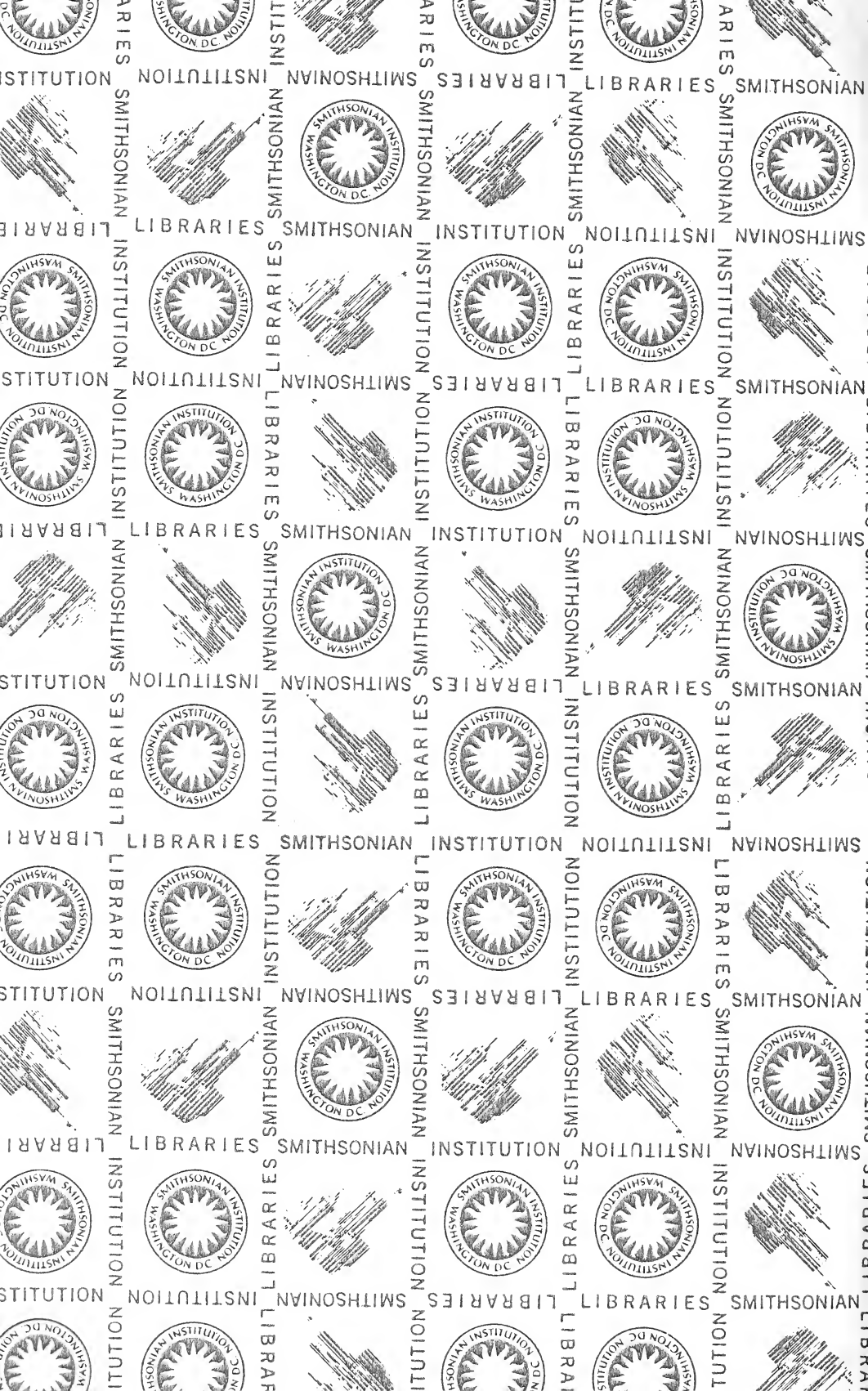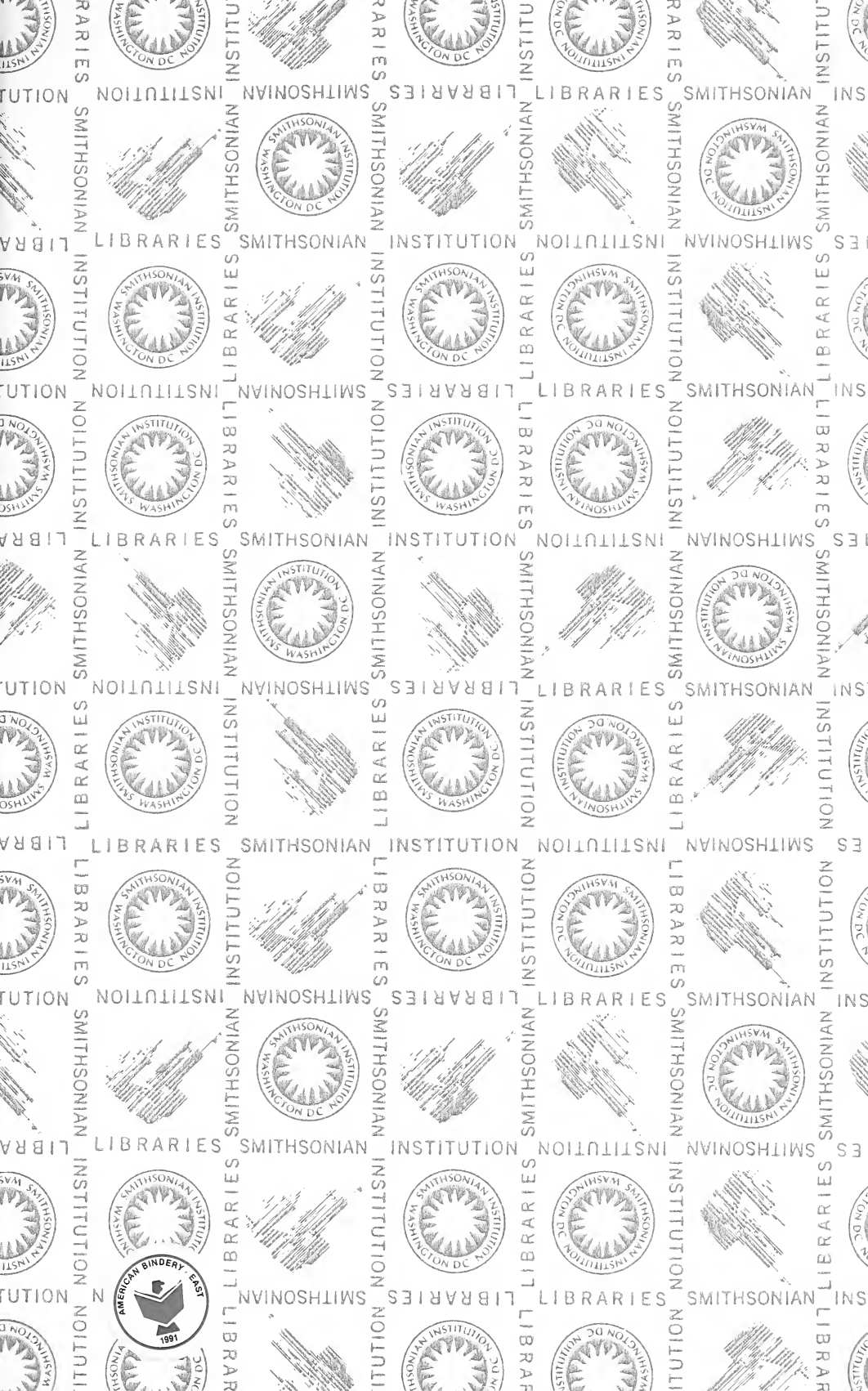# New York Entomological Society

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